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A SYSTEMATIC REVISION OF *BREONIA* (RUBIACEAE–NAUCLEEAE)[1]

Sylvain G. Razafimandimbison[2,3]

Abstract

Breonia A. Rich., a Malagasy endemic genus of the tribe Naucleeae (Rubiaceae, Cinchonoideae), is revised here. The morphology of *Breonia* species is described and compared with that of the other Malagasy Naucleeae, *Breonadia* Ridsdale, *Gyrostipula* J.-F. Leroy, and *Janotia* J.-F. Leroy. *Breonia* is distinguished from these genera by having flattened and elongated placentae, imbricate ovules, and indehiscent, multiple fruits rather than triangular placentae, ovules attached side by side to the base of the placentae, and free, capsular fruits as in these genera. *Neobreonia* Ridsdale is again included in *Breonia*. Twenty species are recognized, including eight that are new to science. A full taxonomic treatment, keys, and distribution maps of the recognized species are provided. The newly described species are illustrated.

Key words: accrescent disk, *Breonia*, Cinchonoideae, floral nectary, Madagascar, Naucleeae, Rubiaceae.

Breonia A. Rich. is a Malagasy endemic genus of the tribe Naucleeae (Cinchonoideae, Rubiaceae) and is the most diverse member of Naucleeae there. Species of *Breonia* are large trees, or rarely shrubs, that occupy habitats ranging from eastern rainforests to western deciduous dry forests as well as swampy forests; they are absent from the semi-arid regions of southern Madagascar. The present revision recognizes 20 species within *Breonia*, of which 8 are newly described herein. *Breonia* is distinguished from the other Malagasy Naucleeae, *Breonadia* Ridsdale, *Gyrostipula* J.-F. Leroy, and *Janotia*

[1] I thank Charlotte Taylor for guiding this revision and generously sharing her knowledge of Rubiaceae with me; my advisor Mick Richardson, Pete Lowry, George Schatz, and James Miller for their advice and support during my stay in St. Louis; Peter Stevens, Toby Kellogg, three anonymous reviewers, and all the members of the E. Desmond Lee molecular systematics lab of the Biology Department of the University of Missouri-Saint Louis for their invaluable comments; Roy Gereau for his help with the Latin diagnoses; Petra De Block, Diane Bridson, and Aaron Davis for their assistance and advice; Trisha Consiglio for her assistance with ArcView; Kendra Sikes for her assistance with the TROPICOS database; David Frodin for sharing his thoughts on the *Cephalanthus chinensis* issues; Raphael Govaerts for sharing his opinions on the Richard and De Candolle issues; Barbara Alongi for her excellent illustrations; MEF and ANGAP for collecting permits; and the following herbaria and their staff for providing loans, access to collections, and/or assistance in the field: BR, K, L, MO, P, PRE, TAN, TEF, and WAG. This research was supported by the Andrew W. Mellon Foundation, the Liz Claiborne Foundation, the Rockefeller Foundation, the Garden Club of Allegheny County State, and the Missouri Botanical Garden. This work was part of my Ph.D. dissertation presented to the Faculty of the Graduate School of the University of Missouri–Saint Louis, U.S.A.
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J.-F. Leroy, by having flattened, elongated placentae, imbricate ovules, and indehiscent, multiple fruits rather than triangular placentae, ovules attached side by side to the base of the placentae, and free, capsular fruits as in these genera. Evidence from recent molecular studies (Razafimandimbison & Bremer, 2002) showed that the monotypic genus *Neobreonia* Ridsdale and *Breonia* sensu Ridsdale together formed a monophyletic group. A more recent phylogenetic study by Razafimandimbison and Bremer (in prep.) based on four data sets (ITS, *rbc*L, *trn*T-L-F, and morphological) placed *Neobreonia* within *Breonia*, making the latter paraphyletic. Both genera have multiple fruits and large accrescent disks. In light of this evidence, I here merge *Neobreonia* with *Breonia*. Both studies also showed that *Breonia* is more closely related to *Breonadia*, *Gyrostipula*, and *Janotia* than it is to the rest of Naucleeae.

Recognition of *Breonia* as a separate genus is widely accepted (e.g., Ridsdale, 1975). However, its circumscription and species limits have been controversial (Haviland, 1897; Homolle, 1938; Ridsdale, 1975). Many more specimens were available for the present study than for earlier studies. Ridsdale's revision was based primarily on the specimens of *Breonia* in the Paris herbarium (P). However, many of the specimens from the Forestry herbarium in Madagascar (TEF) studied here are not held as duplicates in P. Therefore, Ridsdale did not see them.

Materials and Methods

This revision is based on the examination of over 260 herbarium specimens and on field observations of 9 of the 20 *Breonia* species. Specimens from the following herbaria were examined and annotated during this study: BR, K, L, MO, P, PRE, TAN, and TEF (see Appendix 1). All specimens with "SF" meaning "Station Forestière," and "RN" meaning "Réserves Naturelles," were collected by Malagasy technicians under the supervision of the French botanist Réné Capuron. I used the "SF" and "RN" numbers rather than the collector numbers because many specimens of this series do not have collector names on their labels. Also, these are the numbers used in the TROPICOS database of the Missouri Botanical Garden.

Fieldwork was conducted in Madagascar in May–July of 1995 and 1996, respectively, and January–June of 1998 to collect herbarium specimens and pickled material of *Breonia* species, as well as to gather ecogeographical data. The pickled material was preserved in formalin/acetic acid/ethanol, FAA (Radford et al., 1973). This allowed detailed studies of inflorescences and infructescences and revealed a number of important characters, which are impossible to observe in dried specimens.

Table 1. Distinctive fertile morphological features separating *Breonia* and *Sarcocephalus*.

Characters	*Breonia*	*Sarcocephalus*
Inflorescence position	axillary	terminal
Involucral bract	always surrounding the young inflorescence	never surrounding the young inflorescence
Attachment of placentae to septa	to the septal apices	to the middle of the septa
Stigma shape	globose, clavate, capitate	spindle-shaped
Receptive areas on the stigmatic lobe	ca. apical	ca. basal
Accrescent disks	present	absent
Number of ovules per locule	1 to 9	more than 50

Taxonomic History

Identity of *Breonia*

Breonia was originally described by Achille Richard (De Candolle, Sep. 1830); he named the genus after the early 19th century French botanist Jean Nicolas Bréon, one of the first collectors. In 1879, Baillon placed *Breonia* in the synonymy of *Sarcocephalus* Afz. ex Sabine solely because both have multiple fruits, a character that evolved at least three times in Naucleeae (Razafimandimbison & Bremer, 2002). Baillon included two species of *Sarcocephalus*, *S. madagascariensis* (A. Rich.) Baill. and *S. richardiana* Baill., from Madagascar. *Breonia* is quite distinct from *Sarcocephalus* in many aspects (see Table 1). Schumann (1891), Haviland (1897), and Homolle (1938) all endorsed the recognition of *Breonia* as a separate genus. The separation of *Breonia* and *Sarcocephalus* and the monophyly of *Breonia* is strongly supported by ITS and *rbc*L sequence data (Razafimandimbison & Bremer, 2002).

Authorship of *Breonia*

The authorship of *Breonia* has been cited previously as *Breonia* A. Rich. ex DC. (see Ridsdale, 1975, 1978). I disagree with this. Augustin-Pyramus de Candolle asked Achille Richard for a copy of his manuscript of the *Mémoire de la Famille Rubiacées*

Table 2. Species circumscriptions of *Breonia*.

Haviland (1897)	Homolle (1938)	Ridsdale (1975)	Razafimandimbison (2001)
boivinii	*boivinii*	*boivinii*	*boivinii*
coriacea	—[1]	not mentioned	—[4]
cuspidata	*cuspidata*	—[3]	*cuspidata*
longipetiolata	dubious species	dubious species	dubious species
madagascariensis	*madagascariensis*	*madagascariensis*	*madagascariensis*
mauritiana	—[1]	—[3]	—[4]
membranacea	*membranacea*	—[3]	*membranacea*
parvifolia	*parvifolia*	*sphaerantha*	*sphaerantha*
richardiana	*richardiana*	—[3]	—[4]
stipulata	—[1]	—[3]	*stipulata*
	decaryana	*Neobreonia decaryana*	*decaryana*
	havilandiana	—[3]	*havilandiana*
	keliravina	—[5]	—[5]
	louvelii	—[3]	*louvelii*
	macrocarpa	—[2]	*macrocarpa*
	perrieri	*perrieri*	*perrieri*
		citrifolia	*chinensis*
			capuronii
			fragifera
			lowryi
			richardsonii
			sambiranensis
		—[3]	*taolagnaroensis*
			tayloriana
			tsaratananensis

—[1] merged in *B. richardiana*; —[2] merged in *B. madagascariensis*; —[3] merged in *B. citrifolia*; —[4] merged in *B. chinensis*; —[5] merged in *B. decaryana*.

(Richard, Dec. 1830) to avoid any possible nomenclatural conflicts between their work. At that time, Richard's work was already in press for publication. Richard kindly sent De Candolle the manuscript, along with 45 illustrations and later the page proofs, hoping that his work would come out before De Candolle's *Prodromus Systematis Naturalis* (Stearn, 1957). De Candolle was able to cite Richard's work ahead of its actual issue, since the *Prodromus* was published in September 1830 ahead of Richard's book (published in December 1830). Comparison of Richard's original description of *Breonia* with that included in De Candolle's book showed that De Candolle used Richard's description of *Breonia*, but in a different format. The authorship of the genus should remain with Richard. Therefore, I cite *Breonia* as *Breonia* A. Rich. in [DC.].

PREVIOUS SPECIES DELIMITATION IN *BREONIA*

The species limits used by previous authors have been controversial. Haviland (1897), in his first worldwide revision of the tribe Naucleeae, recognized 10 species of *Breonia* (Table 2). He used petiole length and secondary leaf vein number to divide the genus into two major groups: the first group comprising *Breonia madagascariensis*, with subsessile leaves and 12 secondary veins (there are actually 18 or 19 secondary veins, but the leaf blade of the type specimen is folded, so Haviland must have counted what he could see); and the second group containing the remaining species, which had petiolate leaves with 9 to 11 secondary veins. Haviland then used leaf blade length and width, as well as inflorescence width, to delimit the species of his second "petiolate" group. Forty years later, Homolle (1938) adopted new species circumscriptions for *Breonia*. She retained six species from Haviland's treatment, but also described six new species (see Table 2). Unfortunately, she did not provide a key to the species she recognized. Ridsdale (1975) proposed new circumscriptions for *Breonia* based on a combination of the following characters: stipules of terminal vegetative buds conical and obvolute; inflorescences always lateral; calyptra-like bracts coherent, surrounding the young inflorescence, and circumscissile; adjacent calyx tubes free and persistent; calyx lobes densely pubescent; and placentae attached to the upper third of the septum. He used the shape and length of stipules of terminal vegetative buds, the mature stipule length,

and the leaf shape and size as primary characters and recognized only five species (Table 2). He placed *Breonia decaryana* Homolle and *B. kelira-vina* Homolle in his new genus *Neobreonia* because of their partly fused calyx tubes and complanate terminal vegetative buds.

Capuron (1973a), in an unpublished manuscript deposited at P, recognized 13 species using variation in leaf blade size, stipule shape and length, calyx tube length and indumentum, ovule number, and fruit surface. However, he provided neither descriptions of the new species that he recognized nor a key for their identification.

ON THE IDENTITY OF *CEPHALANTHUS CHINENSIS* LAM. AND *ANTHOCEPHALUS* A. RICH.

This section presents the problem of the identity of *Cephalanthus chinensis* Lam. [= *Breonia chinensis* (Lam.) Capuron] and its historical confusion with *Breonia*. This issue has caused a long and controversial debate during the last 30 years (cf. Bakhuizen van den Brink, 1970; Capuron, 1973b; Ridsdale, 1975; Bosser, 1984, 1999).

Lamarck (1785: 678) claimed that a specimen he received from Sonnerat was the type of his *Cephalanthus chinensis*. On the other hand, Richard (Sep. 1830) also stated that he described his *Anthocephalus* [= *Neolamarckia* Bosser] as an Asian, and not Malagasy, monotypic genus (*Anthocephalus indicus*) based on specimens labeled "*C. chinensis* Lam." Lamarck and Richard gave no further details about their type specimens. Bakhuizen van den Brink (1970) and Ridsdale (1975) surmized that the collection of Sonnerat that served as the type of *C. chinensis* was also used by Richard to describe his *Anthocephalus*. Capuron (1973b) and Bosser (1984, 1999) argued that *C. chinensis* Lam. and *Anthocephalus* A. Rich. were not necessarily based on the same specimen.

In the Lamarck herbarium in Paris (P-LA) there is an authentic specimen of *Cephalanthus* with five different labels attached to it. The first label is Lamarck's and says "*Cephalanthus chinensis* enc n° 2." The second label is in Commerson's handwriting (Bosser, 1984), with a short Latin description and the country of origin mentioned as "Isle de France" (i.e., Mauritius). The third label is Sonnerat's and says "c'est la *Morinda* de Chine." The fourth label is also Sonnerat's, on which he wrote "*Morinda* de Chine," and below this name Lamarck added "*Cephalanthus*." The fifth label was written by Roeper and says "*Nauclea purpurea* Roxb." and "*Nauclea orientalis* Lam." This specimen sheet was considered by Capuron (1973b) and Bosser (1984, 1999) to be the type of Lamarck's *Cephalanthus chinensis*. However, Bakhuizen van den Brink (1970) and Ridsdale (1975) disagreed because this specimen does not match Richard's description of *Anthocephalus*. Despite the fact that no one has ever found a collection of *Sonnerat s.n.* in P or P-LA that could have served as the type of both *C. chinensis* Lam. and *Anthocephalus*, Bakhuizen van den Brink and Ridsdale inferred that Lamarck must have based his *C. chinensis* on such a collection. This collection, they further surmized, must contain two elements, one of *Breonia* and the other of *Anthocephalus*. They also argued that Richard must have typified his *Anthocephalus indicus* by only the element of *Anthocephalus* of this hypothetical Sonnerat collection. Bakhuizen van den Brink then typified *Anthocephalus* by only the element of *A. indicus* of this hypothetical Sonnerat collection, excluding its element of *Breonia*. Ridsdale (1975) endorsed Bakhuizen van den Brink's arguments and chose the unverified or non-existent collection as the lectotype of *Anthocephalus*.

Capuron (1973b), followed by Bosser (1984, 1999), disagreed with Bakhuizen van den Brink (1970) and Ridsdale (1975). Capuron and Bosser argued that the type specimen of *Cephalanthus chinensis* Lam. was the specimen with five labels in P-LA because the original description of *C. chinensis* Lam. (Lamarck, 1785: 678) matches this plant, and Lamarck himself annotated it. Bosser argued that Lamarck was apparently influenced by Sonnerat's labels stating "*Morinda* de Chine," and assumed that the plant originally grew in China, the Philippines, and the Moluccas (Bosser, 1984: 244). Bosser then inferred that Sonnerat's label meant that Sonnerat had seen the specimen of *C. chinensis* now in P-LA, and that it reminded him of what he called "*Morinda* de Chine." Bosser (1984) also argued that the second label was Commerson's because there is a similar specimen in P labeled *C. chinensis* Lam. and it was collected by Commerson in Mauritius. In addition, the specimen with five labels in P-LA shows axillary inflorescences and adjacent flowers with fused ovaries that are characteristic of *Breonia*. Capuron (1973b) then concluded that *C. chinensis* Lam. was based on a plant originally from Madagascar rather than Asia, and therefore belongs to *Breonia*. Consequently, Capuron made the new combination *B. chinensis* (Lam.) Capuron.

I agree with Capuron's and Bosser's arguments. A large number of living plant collections of early French botanists (e.g., Chevalier Etienne de Flacourt, Philibert Commerson, Jean Nicolas Bréon, André Michaux, Louis Armand Chapelier) were sent to Mauritius for cultivation in the late 18th

century (Dorr, 1997). Commerson sent a large collection of dried plant specimens to Paris, but these specimens were labeled and distributed to various herbaria only after his death on 13 May 1773 (Dorr, 1997). This may well have caused some confusion between Commerson's and Sonnerat's specimens [see, e.g., Guého (1976) regarding the type of *Phylica nitida* Lam.; Heine (1968) for *Cordia sinensis* Lam.]; the type of *C. chinensis* is apparently another one of these cases.

Bosser (1984) has pointed out correctly that our problem is to find out whether the specimen of *C. chinensis* in P-LA conformed to what Lamarck said in his original description of *C. chinensis*, rather than what Richard said about *Anthocephalus*. Indeed, Bosser argued that Richard may not have seen the specimen of *C. chinensis* in P-LA because Lamarck sold his herbarium to Roeper in 1824 and the entire collection was not returned to Paris until 1886, while Richard's work was in press for publication in 1830. Richard's original description of *Anthocephalus* indicates that he used specimens with flowers and fruit, whereas Lamarck had a specimen with flowers only; therefore, even if Richard had seen the specimen in P-LA, he would still have needed a specimen with fruit. Finally, *Anthocephalus*, as Richard noted, has terminal inflorescences, whereas the specimen of *C. chinensis* in P-LA has axillary inflorescences. Therefore, Bakhuizen van den Brink's and Ridsdale's scenarios of *C. chinensis* being based on mixed elements of *Breonia* of Sonnerat and *Anthocephalus* is untenable, in agreement with Bosser (1999).

Richard's protologue for *Anthocephalus* stated: "Species observata: *Anthocephalus indicus* nob. (*Cephalanthus chinensis* Lam.—*Nauclea purpurea* Roxb.)" (Richard, 1830: 157). Bosser argued that the type specimen of *B. mauritiana* [= *B. chinensis* herein] in P, collected by Commerson (s.n.) in Mauritius, may well have been one of the specimens on which Richard based his *Anthocephalus* because: (1) this specimen has two old labels; the names on the second label are the same names as those in the protologue of *Anthocephalus*; and (2) there is a packet with pieces of an infructescence attached to this specimen, and the separated individual fruits of this infructescence match Richard's description of the infructescence of *Anthocephalus*. Thus, Richard may well have used the fruiting head attached to the type specimen of *B. mauritiana* as part of his original description of *Anthocephalus*. We know only that the element of *Anthocephalus* was attached to the type sheet of *B. mauritiana* when Haviland (1897) described this species: ". . . It is this specimen which has attached to it some heads of *Anthocephalus indicus* and the curious confusion about *Nauclea purpurea* and *Cephalanthus chinensis*." I consider this fruiting head attached to the type specimen of *B. mauritiana* as a piece from the type specimen of Richard's *Anthocephalus indicus*, which is now missing.

In conclusion, *Cephalanthus chinensis* Lam. is *Breonia*, whereas *Anthocephalus* A. Rich. is Asian. Bosser (1984) created a new generic name *Neolamarckia* for the Asian taxa that match Richard's original description of *Anthocephalus*, and made the new combination *Neolamarckia cadamba* (Roxb.) Bosser based on *Nauclea cadamba* Roxb. (1824). I agree with Bosser's combination because *N. cadamba* Roxb. is the older name, and thus it has priority over *A. indicus* A. Rich. (1830). However, Ridsdale (1998), in his treatment of Rubiaceae for Sri Lanka, continued to use *Anthocephalus* rather than *Neolamarckia* for these plants.

Species Circumscriptions in *Breonia* sensu Razafim.

Haviland's (1897) circumscription of *Breonia* species based on secondary leaf veins, leaf blades, and inflorescences is problematic because these characters overlap for some well-defined species. Using such features as stipules of terminal vegetative bud size, mature stipule length, and leaf shape and size as primary discriminating characters forced Ridsdale to lump taxa and recognize only five species, of which three (*Breonia citrifolia*, *B. madagascariensis*, and *B. sphaerantha*) become rather heterogeneous. Neither Haviland (1897) nor Ridsdale (1975) used floral and fruit characters for their keys for *Breonia*. However, there are a number of useful taxonomic characters, such as shapes of the stipules of the terminal vegetative bud and inflorescence axis, corolla lobe indumentum, the degree of fusion of adjacent ovaries, accrescent disks, and infructescence surfaces. As a result, I abandon Haviland's (1897) and Ridsdale's (1975) species delimitations and adopt here new species limits within *Breonia*.

My criterion for recognizing species is the presence of one or more apparently fixed or non-overlapping morphological differences between putative species. Morphologically distinct groups of specimens were identified and delimited by non-overlapping or fixed diagnostic differences; these diagnosable morphological units, which I refer to as species, are hypotheses until new data are available to refute them. To relate this functional species concept to more theoretical ones, one must test it on the basis of the criteria defining each theoretical species concept.

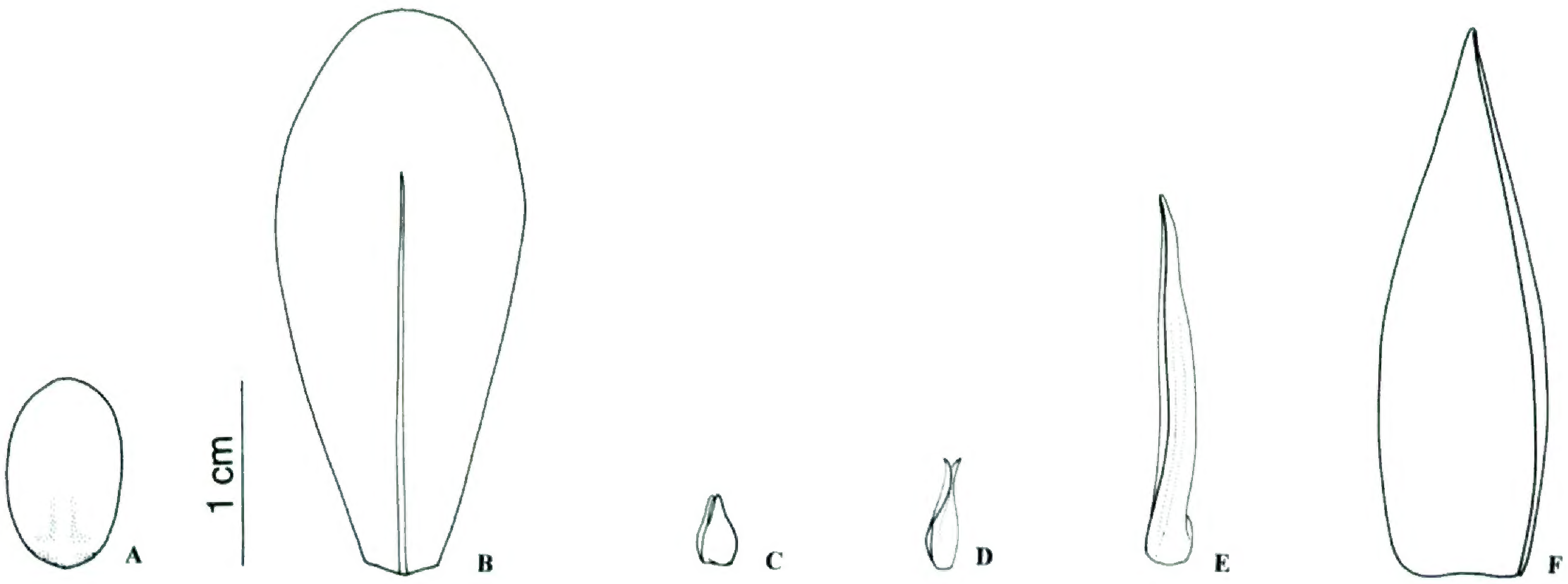

Figure 1. Variation in shape and size of the stipules of the vegetative buds in *Breonia* (A, C–F) and *Janotia*.—A *Breonia decaryana*.—B. *Janotia macrostipula*.—C. *B. capuronii*.—D. *B. chinensis*.—E. *B. stipulata*.—F. *B. madagascariensis*.

Morphology and Taxonomic Characters of *Breonia*

A detailed overview of the morphological characters of *Breonia* species is presented as well as their taxonomic significance. The allied Malagasy genera *Breonadia*, *Gyrostipula*, and *Janotia* are also discussed for comparison.

HABIT

Plants of *Breonia* are medium to large, sometimes emergent trees up to 30 m tall, rarely shrubs. Buttresses are reported in *Breonia sphaerantha*. The bark is smooth to rugose. The trunk is typically straight. The branches are usually plagiotropic.

LEAVES

Breonia leaves are simple, opposite, and decussate, as in most Rubiaceae, and generally coriaceous to membranaceous. The length of petioles and the size of leaf blades are useful for recognizing some species. The leaves of *Breonia* are petiolate or rarely subsessile (*B. madagascariensis*). Most species have small to medium-sized leaves, but two species (*B. macrocarpa* and *B. madagascariensis*) have relatively large leaf blades: the former to 38 × 25 cm, and the latter up to 45 × 35 cm. The leaf blades are mostly glabrous, or rarely pubescent in a few individuals of *B. perrieri*. *Breonia macrocarpa* is characterized by having brown, long hairs on the lower surface of the leaf blades.

Domatia. Domatia are cavities located in the axils of veins on the abaxial sides of leaf blades (Jacobs, 1966). They typically occur in the axils of secondary veins in most species of *Breonia*. Mites or mite eggs can be found in the domatia, although the occurrence of domatia is not dependent on the arachnid presence; these domatia may provide the host plant protection from herbivores or pathogens (Pemberton & Turner, 1989). The type and location of domatia are useful for species delimitation in *Breonia*. In *B. macrocarpa*, they occur in the axils of the secondary and tertiary veins. Both secondary and tertiary domatia have never been seen in other Naucleeae; they are only known in a few members of Rubiaceae (e.g., *Aoranthe*, *Pleiocoryne*, *Oligocodon*) (Robbrecht, 1988). In *Breonia*, domatia can be tufts (covered by dense hairs), or cryptic and glabrous, or pits (depressions in the lamina with a broad opening).

Venation. The venation of the leaf blades is usually prominulous on the upper sides of the leaf blades, but is prominent in *Breonia havilandiana*, *B. madagascariensis*, and *B. tsaratananensis*. The secondary venation is usually eucamptodromous (Radford et al., 1973).

Stipules of terminal vegetative buds. The stipules of terminal vegetative buds are usually conical and obvolute in most *Breonia* species (Fig. 1C–F). In these, two stipules overlap in the bud such that one half of each is external and the other half is internal (Harris & Harris, 1994). Their sizes and lengths vary between species, which is useful for their identification. In *Breonia decaryana* and *Janotia macrostipula*, the stipules of terminal vegetative buds are complanate (Fig. 1A, B), the two stipules being flat and pressed together. In *Gyrostipula*, they are long, filiform, and convolute, one stipule being rolled inside another (Radford et al., 1973).

Mature stipules. The stipules of *Breonia* and other Malagasy Naucleeae are interpetiolar, boat-shaped (cymbiform), and usually abaxially carinate. The keels are prominulous in many species and prominent in *B. tayloriana* and *B. madagascarien-*

sis. In *Gyrostipula,* the stipules are without keels and are twisted when dry. The size and persistence of the stipules vary among species of *Breonia* and are useful for species distinction. Stipules are typically deciduous in *Breonia.* In *Breonia tayloriana,* they are semi-persistent.

INFLORESCENCES

Like other Naucleeae, *Breonia* species have globose inflorescences on which numerous small flowers (usually more than 50) form dense clusters rather than capitate inflorescences found in other Rubiaceae (e.g., Schradereae, Psychotrieae). The individual flowers are inconspicuous, and the entire cluster of flowers acts as a single attractive unit.

Inflorescence stalk. In *Breonia,* the inflorescence stalk is typically articulate and composed of a peduncle, a node, and an inflorescence axis (e.g., Figs. 6F, 9E, 14C). Ridsdale (1975) used the term "flowering axes" to refer to what I call inflorescence axes; he called "true peduncles" what I refer to as peduncles. An evident node separates the peduncle from the inflorescence axis. The inflorescence axis is located between the branch bearing the inflorescence and the node. The peduncle is located between the node and the base of the head; this is hidden by the bracts prior to the separation of the bract lobes. The peduncle can be absent (e.g., Figs. 15A, 16F); in some species (e.g., Fig. 6F, *Breonia capuronii; B. decaryana*), this continues to elongate after the inflorescence axis has finished growing at the end of anthesis. The length and shape of the inflorescence axes are useful for recognizing species in *Breonia.* Inflorescence axis shapes can be terete (e.g., *Breonia capuronii, B. perrieri, B. richardsonii, B. sphaerantha*) or flattened (e.g., *B. chinensis, B. havilandiana, B. membranacea, B. stipulata,* and *B. tayloriana*). The inflorescence axes are usually longer than the peduncles; however, in *Breonia decaryana, B. capuronii,* and *B. sphaerantha,* the two are similar in size and shape.

Bracts. Most *Breonia* species have bracts that are coherent, but histologically distinct (Radford et al., 1973), valvate, and completely enclose the young inflorescence in a calyptra-like fashion. As the inflorescences develop, the bracts separate longitudinally into two lobes on the nodes lasting for only a few days and usually falling off before anthesis. They may persist for two or three weeks after anthesis in *Breonadia, Gyrostipula,* and *Breonia decaryana.* In *B. richardsonii,* the bracts are tubular, appressed to the inflorescence axis, and terminated by three to four broadly triangular lobes. They never enclose the young inflorescence. This is unique in *Breonia* and the whole of Naucleeae. Finally, the bracts in *Breonia* are usually glabrous, except in *B. macrocarpa* and *B. tsaratananensis,* where they are densely pubescent. The position of the bract varies depending on whether or not the peduncle continues to elongate after the inflorescence axis ends its elongation. When the peduncle does not elongate, the bract lies immediately below the inflorescence, as in *B. chinensis, B. cuspidata, B. madagascariensis,* and *B. taolagnaroensis.*

Ridsdale's (1975) descriptions of calyptra-like bracts of *Breonia* being coherent, surrounding the young inflorescence, and circumscissile, appear to be incorrect. I have seen two herbarium specimens of *Breonia chinensis* showing circumscissile calyptra-like bracts. In several species, including *B. chinensis, B. havilandiana, B. macrocarpa, B. membranacea,* and *B. tsaratananensis,* the bracts normally separate longitudinally into two equal hemispheres. This apparent circumscissile rupturing of the bracts evidently happens during specimen preparation. The illustration of *Sarcocephalus richardii* Drake [= *Breonia chinensis* (Lam.) Capuron] in Grandidier (1897: 457) shows the circumscissile calyptra-like rupturing of the bract. It is possible that Ridsdale (1975) was influenced by this illustration.

Interfloral bracteoles are absent in *Breonia,* as well as in *Gyrostipula* and *Janotia.* However, they are present in *Breonadia.* In *Breonia richardsonii* (Fig. 14F), the ovary bases are surrounded by long hairs.

FLOWERS

The flowers in *Breonia* are actinomorphic, hermaphroditic, protandrous, sessile, and usually 5-merous, although 4-merous examples are occasionally encountered. The flowers are typically 4-merous in *B. capuronii, B. decaryana, B. fragifera,* and *B. sphaerantha.*

Calyx. The calyx tubes (i.e., tubular parts of limb above the hypanthium) in most *Breonia* species are free from each other and clearly visible. In *B. fragifera* and *B. decaryana* the calyces are barely evident. These calyx tubes of adjacent flowers are only partly fused in *B. decaryana;* they are completely fused in *B. fragifera.* Therefore, the degree of calyx fusion is useful for species recognition in *Breonia.*

The shape and surface of the calyx tubes are useful at the species level. In *Breonia chinensis, B. lowryi, B. tayloriana, B. stipulata,* and *B. taolagnaroensis,* the calyx tubes are infundibular and smooth. Other species have infundibular and

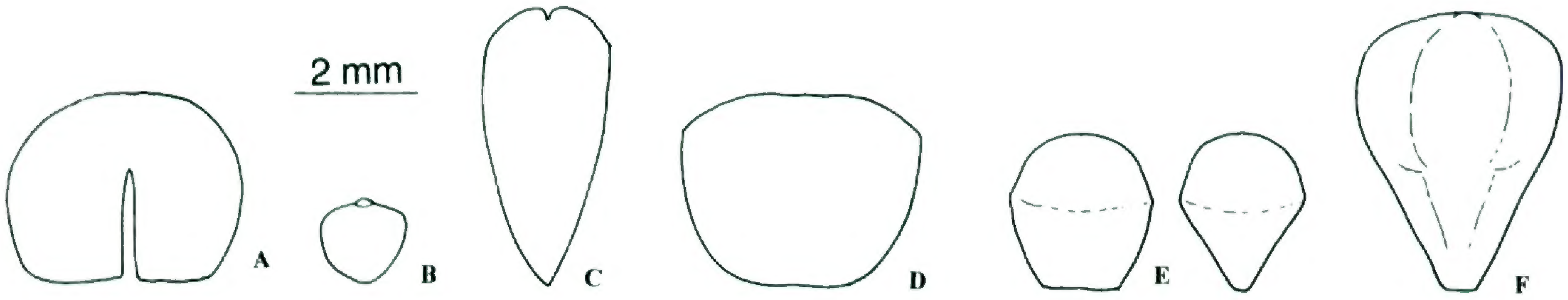

Figure 2. Different shapes of accrescent disks in *Breonia* fruits. —A. *Breonia decaryana.*—B. *B. sphaerantha.*—C. *B. fragifera.*—D. *B. macrocarpa.*—E. *B. chinensis.*—F. *B. taolagnaroensis.*

ribbed calyx tubes. The ribs may be prominulous (e.g., *B. sambiranensis*) or prominent (*B. tsaratananensis* and *B. boivinii*). In *B. tsaratananensis* the calyx tubes are constricted above the middle and narrowed toward the base and the lobes; this is unique in *Breonia.*

The shape of the calyx lobes varies from oblong to triangular, sometimes with truncate apices. *Breonia sambiranensis* has a distinct calyx lobe shape: short, truncate, with a shallow depression in the center and a short appendage on the edge toward the style (Fig. 14D). Broadly triangular and pubescent lobes characterize *Gyrostipula,* while *Breonadia* and *Janotia* have long, linear, pubescent lobes.

Corolla. The corolla of *Breonia* is always hypocrateriform and yellow-tinged. In *B. boivinii, B. sambiranensis,* and *B. tsaratananensis,* some of the corolla lobes have dorsal protuberances (e.g., see *B. sambiranensis,* Fig. 14E). Corolla indumentum is useful for species recognition. One species group (*B. chinensis, B. cuspidata, B. louvelii, B. membranacea, B. stipulata,* and *B. taolagnaroensis*) has glabrous lobes. *Breonia boivinii, B. sambiranensis,* and *B. tsaratananensis* all have pubescent or puberulous lobes. In *B. macrocarpa* and *B. madagascariensis* lobes are puberulous and marginally glabrate.

Nectaries. As in other members of Naucleeae sensu Razafimandimbison and Bremer (2002), the floral nectaries (i.e., disks) in *Breonia* are inconspicuous, surround the style base, and are embedded in the hypanthia between the base of the corolla tube and the top of the ovary. For all *Breonia,* nectaries continue to grow during infructescence development and become hardened and conspicuous. I call such nectaries "accrescent disks." Capuron, in his unpublished treatment for Malagasy Rubiaceae at P, also observed this type of disk in *Breonia* but did not understand its nature. These accrescent disks appear to be the single synapomorphy among members of Malagasy Naucleeae. However, they tend to be much larger in *Breonia* species than in *Breonadia, Gyrostipula,* and *Janotia.* The shape of these accrescent disks (Fig. 2) varies from obconical to obtriangular, to pentagonal or rounded. Their shape and size are useful for species distinction. This is the first report of the use of this character in the classification of *Breonia* as well as in Rubiaceae.

Stamens. *Breonia* filaments are usually very short and flattened; they are inserted in the throat of the corolla tubes and sometimes slightly exserted. The anthers are always bicuspid at the base, basifixed, introrse, dehiscing along longitudinal slits.

Gynoecium. In *Breonia,* ovaries (hypanthia) of individual flowers are always bicarpellate. They are coherent and nonseptate in *Breonia capuronii, B. decaryana, B. fragifera,* and *B. sphaerantha* (see Figs. 6D, 9F), whereas they are fused (syncarpous) and septate in the remaining species. Adjacent ovaries are typically fused. However, in *B. richardsonii,* prior to and during anthesis the ovaries are fused only at the base, but as the development continues, the fusion extends to the mid-point (post-genital fusion), producing multiple fruits (Radford et al., 1973). Ovule number varies from 1 to 9; all four nonseptate and three of the septate species (*B. cuspidata, B. louvelii,* and *B. taolagnaroensis*) are uniovulate; the remaining 13 septate species are multiovulate.

Placenta size and shape vary between species in *Breonia.* The uniovulate species have small and ovate placentae (Fig. 9F), whereas the multiovulate species have large, flattened, and elongated ones (Fig. 3C, D). The placentae are triangular in *Breonadia, Gyrostipula,* and *Janotia* (Fig. 3A, B). Placentae are usually apically attached to the septum, and adnate to the lateral sides of the nectaries, located in the distal center portions of the carpels (see Fig. 13H). These two characters are useful for recognizing *Breonia* from the other Malagasy genera of Naucleeae, but have never been used for classification by earlier authors. Defining *Breonia* by the placentae attached to the upper third of the septum as originally done by Haviland (1897) in

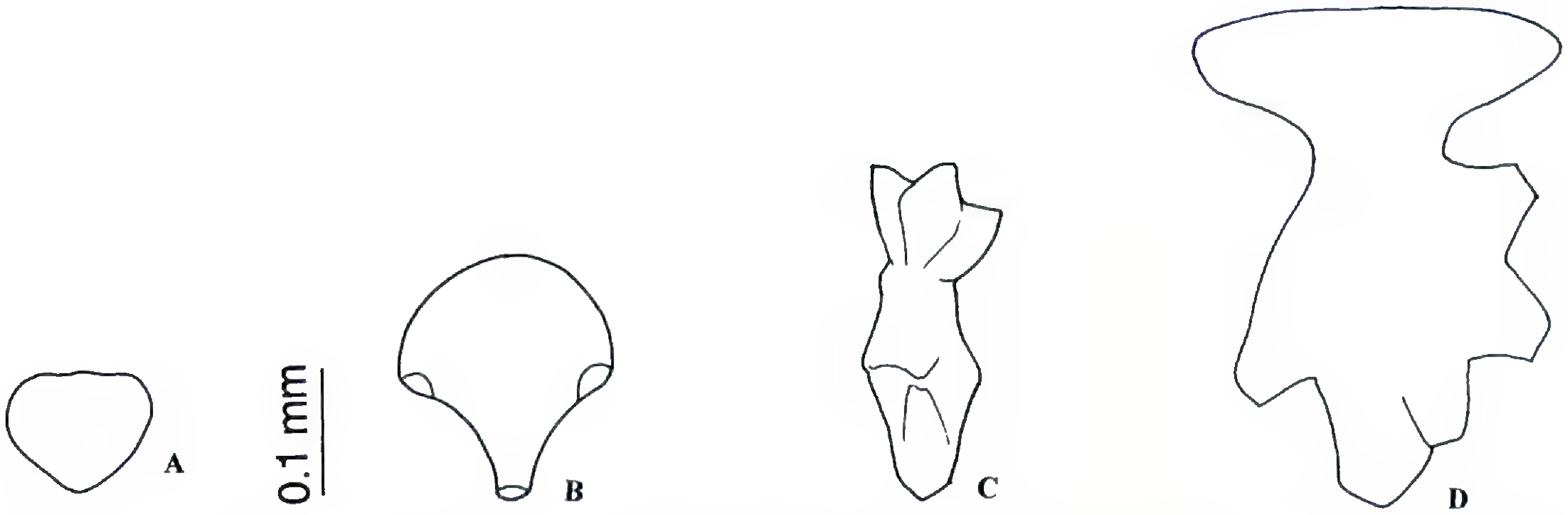

Figure 3. Different shapes of placentae in *Breonia* (C, D) and its allies (A, B). —A. *Gyrostipula foveolata.*—B. *Breonadia salicina.*—C. *Breonia sambiranensis.*—D. *B. macrocarpa.*

his first worldwide revision of Naucleeae, and later by Ridsdale (1975), appears to be incorrect.

Ovule attachment to the placenta is another useful character that distinguishes *Breonia* from *Breonadia, Gyrostipula,* and *Janotia.* In *Breonia,* the ovules are flattened and imbricate (Fig. 4D) along the length of the placentae; they are attached side by side at the base of the placenta in *Breonadia, Gyrostipula,* and *Janotia* (Fig. 4A–C).

Breonia stigmas are typically globose to clavate, or rarely capitate, pollen presenters. The receptive areas are always restricted to the top of the stigmatic lobe.

INFRUCTESCENCES

In *Breonia* species the infructescences develop from syncarpous ovaries to form multiple fruits that are fleshy, almost woody, when dry. They are ornamented by accrescent calyces in most species. In *B. fragifera* and *B. decaryana,* the calyx remnants are barely evident and their infructescence surfaces are pusticulate (with small, broad, slight elevations not high or abundant) and rugose, respectively. In *Breonia,* all the fruits are fused and constitute multiple fruits; the individual fruits are berry-like, bearing 1 to 9 seeds completely enclosed by thin exocarps and thick, hard endocarps.

SEEDS

In *Breonia,* the seeds are usually strongly flattened ellipsoid. Concavo-convex seeds are found in *Breonia chinensis* and *B. stipulata. Breonia* seeds are usually unwinged, although rudimentary wings are sometimes observed at both ends (e.g., *B. chinensis* and *B. taolagnaroensis*), or only at the base (e.g., *B. perrieri*). The seeds are possibly released when the corky accrescent disks fall off (see the section on seed dispersal). These disks can be easily removed when the infructescences are still fresh, or after soaking dried ones for several hours. Seed-coat is lineate (e.g., Fig. 6C) in the nonseptate species, and typically reticulate (e.g., Figs. 9C, D, 11C, 14H, 16E) in the septate species.

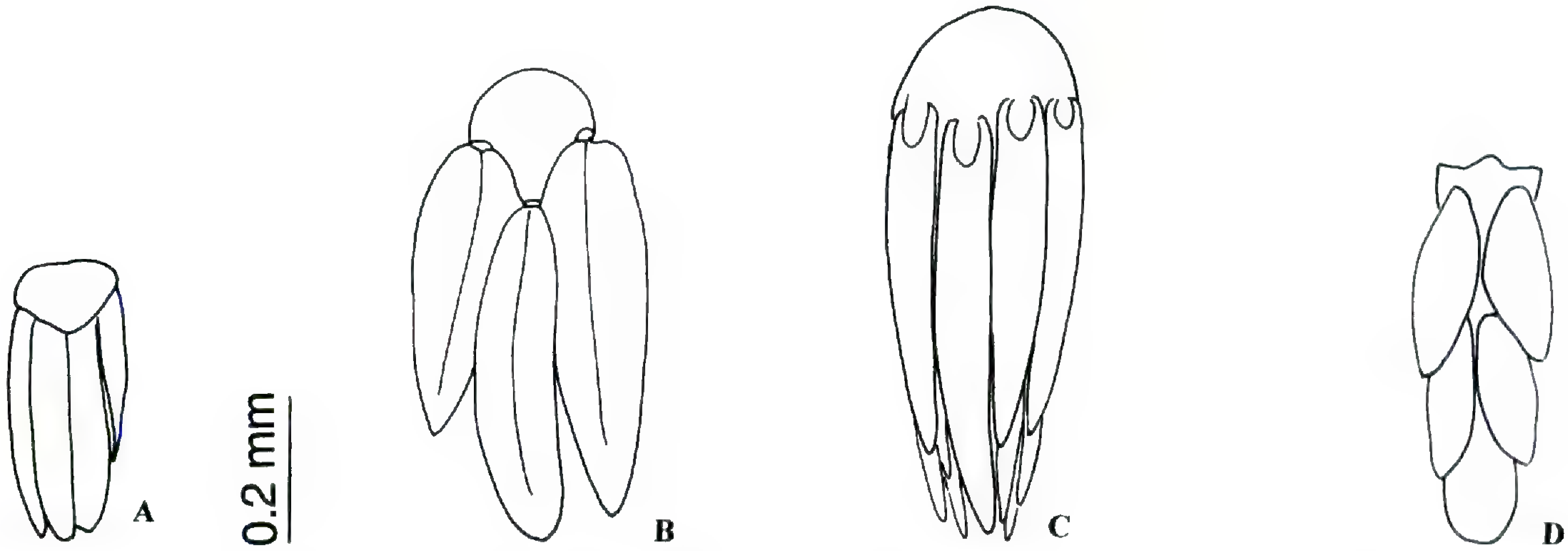

Figure 4. Ovule attachments to placentae in *Breonia* and its allies (A–C). —A. *Gyrostipula foveolata.*—B. *Breonadia salicina.*—C. *Janotia macrostipula.*—D. *Breonia sambiranensis.*

Ecology

Pollination Ecology

How *Breonia* pollinates remains unknown. In the Ankarana Reserve (northern Madagascar) in 1998 I saw the beginning of anthesis in a young individual plant of *B. perrieri.* Flowers in each inflorescence opened simultaneously to emit an intense odor of nectar, which might attract visitors from considerable distance. The plant was visited by several honeybees for a few hours.

Diaspore Dispersal

Entire infructescences. In *Breonia,* the entire infructescence can function as a dispersal unit. In 1998, I observed in the Anjanaharibe Sud Reserve (northeastern Madagascar) a number of mature infructescences of *B. chinensis,* a facultative rheophyte, floating on the river. The corky accrescent disks may act as flotation devices allowing the infructescences to float until they reach the riverbank, where they may be eaten by any frugivores. After flower fall, the nectaries have a new function, as cork-like seed releasers.

A different floating device has also been reported on the seed-coat of the African Naucleeae *Sarcocephalus pobeguinii* Pob. ex. Pell., which is a facultative rheophyte (Abbiw, 1985). Abbiw collected mature seeds of *Nauclea diderrichii* (De Wild. & T. Durand) Merr. and *Sarcocephalus latifolius* (Smith) Bruce (both terrestrial species), as well as *S. pobeguinii.* A simple experiment was performed by soaking the seeds of each species in separate containers of water. After 24 hours, the water was poured off: seeds of *Nauclea diderrichii* and *S. latifolius* lay at the bottom of the containers, whereas those of *S. pobeguinii* were still floating. *Nauclea diderrichii* and *S. latifolius* seeds were noted to sink after only a few minutes of immersion. The seed-coat apparently acts as a floating device preventing the seeds from sinking.

Seeds. Infructescences of *Breonia* are used as food by all species of Malagasy lemurs. In Lokobe Reserve (Nosy Be District, Antsiranana Province, in northern Madagascar), *B. boivinii* and *B. sambiranensis* were the second most important food item in the diet of the black lemur (*Eulemur macaco*) in early 1992. Thirteen percent and 25% of its feeding time during January and February, respectively, were spent on these two species of *Breonia* (Birkinshaw, 1995). Birkinshaw frequently observed intact seeds of *B. boivinii* and *B. sambiranensis* in lemur droppings. He found that 2 of 7 defecated seeds germinated, compared with 7 of 30 seeds collected from the ripe infructescences used as a control. The mature infructescences were not observed to be eaten by any other frugivores in the Lokobe Reserve. Both species of *Breonia* also occur in the Ambanja region where *Eulemur macaco* is also known to be common, suggesting that *E. macaco* may be an effective agent of seed dispersal for *B. boivinii* and *B. sambiranensis.* Notably, *B. sambiranensis* is known from only two specimens outside of the Sambirano regions. Seed dispersal mechanisms for other *Breonia* species remain unknown.

Economic Uses

All Malagasy Naucleeae are known under the local name "Valotra" or "Valotro," meaning that which is reserved for a particular use (Boiteau, 1985). From the 19th century through the mid 20th century, the Malagasy Naucleeae were used for posts placed around villages to protect against enemies. All *Breonia* have various local uses such as boats, bridges, making handcrafts and furniture, and for general construction purposes because they produce high-quality, hard wood. Several species are used medicinally. The infructescences of *Breonia* are eaten by animals and humans.

Systematic Position of *Breonia* sensu Razafim. in Naucleeae sensu Razafim. & Bremer

Breonia has been placed in quite different tribes over the last 170 years. Richard (1830) and De Candolle (1830) placed *Breonia* in the tribe Operculareae along with other tribes with pluriovular locules. Endlicher (1841) placed the genus in his subtribe Sarcocephalinae (of the tribe Gardenieae), along with *Sarcocephalus, Zuccarinia* Blume [= *Jackiopsis* Ridsdale], *Lucinaea* DC. [= *Schradera* Vahl], and *Canephora* Juss. Schumann (1891), followed by Haviland (1897), Verdcourt (1958), Ridsdale (1975), and Robbrecht (1988, 1994), placed *Breonia* in the tribe Naucleeae based on its compact spherical inflorescences. However, Bremekamp (1966) transferred *Breonia,* along with *Adina* Salisb., *Mitragyna* Korth., *Uncaria* Schreb., and *Neonauclea* Merrill, from the tribe Naucleeae to the tribe Cinchoneae, arguing that they differ from the other genera of Cinchoneae in the capituliform inflorescence only. All these genera, with the exception of *Breonia,* have capsular fruits with winged seeds, which are characteristic of Cinchoneae. Bremekamp provisionally placed these genera in a separate subtribe within Cinchoneae based on their capituliform inflorescences. Evidence from recent molecular studies based on ITS and *rbc*L sequence data (Razafimandimbison & Bremer, 2002) strongly suggests that *Breonia* belongs to Naucleeae

and is closely related to the other Malagasy genera *Breonadia, Gyrostipula,* and *Janotia.* It is worth noting that one species of African *Uncaria, U. africana* var. *africana,* is also present in Madagascar. These five genera can be identified using the key below.

KEY TO THE GENERA OF MALAGASY NAUCLEEAE

1a. Climbers, paired fang hooks present .... *Uncaria* Schreb. (1 species)
1b. Trees or shrubs, paired fang hooks absent.
  2a. Hypanthia of the adjacent flowers fused or at least at the base; fruits fused, indehiscent .... *Breonia* A. Rich. (20 species)
  2b. Hypanthia of the adjacent flowers free; fruits free, dehiscent.
    3a. Leaves verticillate; stipules intrapetiolar; interfloral bracteoles present; seeds unwinged .... *Breonadia* Ridsdale (monotypic)
    3b. Leaves opposite; stipules interpetiolar; interfloral bracteoles absent; seeds winged.
      4a. Leaf blades 20–27 × 8–10 cm; stipules of the terminal vegetative buds flattened, complanate; stipules persistent .... *Janotia* J.-F. Leroy (monotypic)
      4b. Leaf blades 8–10 × 3–5 cm; stipules of the terminal vegetative buds convolute; stipules deciduous .... *Gyrostipula* J.-F. Leroy (2 species, 1 of which is yet to be described)

RELATIONSHIPS AMONG SPECIES

Species of *Breonia* can be subdivided into two distinct groups based on the following characters: (1) a group with reduced calyces, coherent carpels, non-septate, and with lineate seed-coat (*Breonia capuronii, B. decaryana, B. fragifera,* and *B. sphaerantha*); and (2) a group with well-developed calyces, syncarpous carpels, septate, and with reticulate seed-coat (remaining species). The monophyly of these two groups needs to be tested using fast-evolving markers.

The included key to *Breonia* species does not reflect the above relationships; instead, I propose a more practical key that puts more emphasis on the most obvious unique vegetative character states, such as the shape and arrangement of the stipules of the terminal vegetative buds and size of leaf blades.

TAXONOMIC TREATMENT

Breonia A. Rich., in DC., Prodr. 4: 620. Sep. 1830. TYPE: *Breonia madagascariensis* A. Rich.

Cephalidium A. Rich., Mém. Fam. Rubiacées. 210. Dec. 1830. TYPE: *Cephalidium citrifolium* A. Rich. [= *Breonia chinensis*].
Franchetia Baill., Bull. Mens. Soc. Linn. Paris 1: 477. 1885. TYPE: *Franchetia sphaerantha* Baill. [= *B. sphaerantha*].
Elattospermum Sol., Bull. Herb. Boissier 1: 277. 1893. TYPE: *Elattospermum longipetiolatum* Sol. [= *B. sphaerantha*].
Neobreonia Ridsdale, Blumea 22: 546. 1975. TYPE: *Breonia decaryana* Homolle.

Trees or emergent trees, or rarely shrubs. Bark gray. Stipules of terminal vegetative buds conical or rarely ovate to obovate, obvolute or rarely complanate, glabrous or pubescent. Leaves simple, opposite, decussate, persistent or deciduous; domatia present in axils of secondary veins or rarely tertiary veins or absent; stipules interpetiolar, mostly cymbiform or rarely complanate, deciduous or rarely semi-persistent, entire. Inflorescences usually solitary or sometimes 2 or rarely 4 to 8 per axil, axillary, globose; inflorescence axes unbranched or rarely branched, flattened or terete, usually slender or rarely robust and woody, glabrous to pubescent, articulated or not; bracts usually calyptra-like, cohering and completely enclosing the young inflorescence, separating longitudinally into two equal hemispherical shells, remaining attached to the node for a few days and then falling off; peduncles elongated (as internode above the inflorescence axis) or not. Flowers hermaphroditic, radially symmetrical, mostly 5-merous or sometimes 4-merous, closely congested, sessile; calyx tubes infundibular, inside usually densely pubescent, outside glabrous except for a few straight long hairs around the base, free from others or rarely fused; calyx lobes oblong to truncate, densely pubescent; corolla tubes hypocrateriform, inside glabrous to puberulous, outside glabrous; corolla lobes oblong, glabrous or puberulous to pubescent, aestivation imbricate in bud; stamens 5 or rarely 4, inserted on the throat of the corolla tubes; anthers introrse, partly exserted, dehiscing by longitudinal slits, basifixed; filaments short, flattened, glabrous; stigmas 1 per flower, clavate to globose or slightly cylindrical, exserted from the corolla tubes, pollen presenters; receptive areas restricted to the top of the stigmatic lobe; ovary of an individual flower always bicarpellate, syncarpous or coherent, adjacent ovaries typically syncarpous or rarely fused at the base; ovules 1 to 9 per locule, strongly flattened, pendulous, imbricate; placentae apically attached to the septum, usually elongated, flattened, adnate to the septum; floral nectary epigynous, embedded in the hypanthium between the base of the corolla tube and the apex of the ovary. Infructescences formed by multiple fruits, globose, with persistent calyx remnants. Individual fruits berry-like; endocarps hard and glossy or sometimes fibrous and soft; disks accrescent, conspicuous, variable in size; seeds usually strongly flattened, sometimes concavo-convex, or plano-convex, ellipsoid, not alate or rarely with rudimentary wings, red; seed-coat reticulate or lineate.

Key to *Breonia* Species

1a. Stipules of terminal vegetative buds flattened, complanate; inflorescences 4 to 8 per axil .... 5. *B. decaryana*
1b. Stipules of terminal vegetative buds conical, obvolute; inflorescences usually 1 or rarely 2 per axil.
  2a. Lower surfaces of leaf blades always pubescent, tuft-domatia present in the axils of secondary and tertiary veins .... 10. *B. macrocarpa*
  2b. Lower surfaces of leaf blades always glabrous, tuft-domatia absent in the axils of secondary and tertiary veins.
    3a. Leaf blades 45 × 25 cm; inflorescence axes 16–21 cm long .... 11. *B. madagascariensis*
    3b. Leaf blades less than 32 × 16 cm; inflorescence axes less than 13 cm long.
      4a. Stipules semi-persistent .... 19. *B. tayloriana*
      4b. Stipules deciduous.
        5a. Leaf blades with the 3 secondary veins diverging from the base of the midrib, base cordate .... 13. *B. perrieri*
        5b. Leaf blades without 3 secondary veins diverging from the base of the midrib, base noncordate.
          6a. Bracts tubular, terminated by 3 or 4 broadly triangular lobes, never surrounding the young inflorescence, persistent; adjacent ovaries fused at the base only .... 14. *B. richardsonii*
          6b. Bracts calyptra-like, surrounding the young inflorescence, deciduous; adjacent ovaries completely fused.
            7a. Adjacent calyx tubes completely fused; infructescences with barely evident calyx remnants .... 6. *B. fragifera*
            7b. Adjacent calyx tubes free; infructescences with well-developed calyx remnants.
              8a. Corolla lobes pubescent to puberulous, recurved.
                9a. Leaf blades with glabrous cryptic-type domatia on lower surface, swollen on upper surface; fertile peduncles densely pubescent; calyx tubes uniquely dilated above the middle and constricted at both ends .... 20. *B. tsaratananensis*
                9b. Leaf blades without domatia; fertile peduncles glabrous; calyx tubes funnel-shaped.
                  10a. Lower surfaces of leaf blades yellow-red-tinged when dry; calyx tubes 1–1.2 mm long; lobes 0.2–0.3 mm long, bearing shallow depressions on the center and a short protuberance on the edge toward the style .... 15. *B. sambiranensis*
                  10b. Lower surfaces brown-tinged when dry; calyx tubes 2.5–3 mm long; lobes 2–2.2 mm long, without shallow depressions, without protuberance .... 1. *B. boivinii*
              8b. Corolla lobes glabrous and not recurved.
                11a. Inflorescence axes terete; ovaries coherent but not histologically fused, nonseptate.
                  12a. Petioles 1.5–2 cm long; secondary veins drying red-tinged .... 16. *B. sphaerantha*
                  12b. Petioles always more than 2 cm long; secondary veins drying yellow-tinged .... 2. *B. capuronii*
                11b. Inflorescence axes flattened; ovaries fused, septate.
                  13a. Stipules of terminal vegetative buds 15–22 mm long.
                    14a. Leaf blades obovate, always wavy when dry .... 7. *B. havilandiana*
                    14b. Leaf blades elliptic to lanceolate, not wavy when dry .... 17. *B. stipulata*
                  13b. Stipules of terminal vegetative buds 4–10 mm long.
                    15a. Ovaries uniovulate.
                      16a. Leaf blades 9–16 × 3.5–6.5 cm long, ovate to oblong in shape .... 18. *B. taolagnaroensis*
                      16b. Leaf blades 4–9 × 1.5–3.5 cm long, oblanceolate in shape.
                        17a. Leaf blade apices acute, base cuneate; fertile peduncles 2–4 cm long .... 8. *B. louvelii*
                        17b. Leaf blade apices caudate, bases attenuate; fertile peduncles 4.5–6.5 cm long .... 4. *B. cuspidata*
                    15b. Ovaries multiovulate (2 to 9 ovules per locule).
                      18a. Petioles 3–6 mm long .... 12. *B. membranacea*
                      18b. Petioles at least 9 mm long.

19a. Stipules of terminal vegetative buds more than 5–6 mm long; inside of calyx tubes pubescent; 2–4 ovules per locule .... 3. *B. chinensis*

19b. Stipules of terminal vegetative buds 3 mm long; inside of calyx tubes glabrous; more numerous ovules (7–9) per locule .... 9. *B. lowryi*

1. **Breonia boivinii** Havil., J. Linn. Soc. Bot. 33: 35. 1897. TYPE: Madagascar. [Antsiranana province], District Nosy be [without exact locality], *Boivin s.n.* (holotype, K!; isotype, P not seen).

Shrubs, ca. 7 m tall. Bark rugose. Leafy stems terete, glabrous. Stipules of terminal vegetative buds conical, 5–7 × ca. 5 mm, glabrous. Leaves persistent; petioles (10–)15–25 × ca. 4 mm, terete, glabrous; blades 11.5–23 × 4.5–13.5 cm, ovate to broadly obovate, glabrous, coriaceous, glossy, apex acute to rounded, base cuneate, lower surfaces brown-tinged when dry; margins glabrous, entire; secondary veins ca. 9 pairs per side, eucamptodromous; tuft-type domatia in the axils of midribs or absent; stipules 6–9 × ca. 6 mm, cymbiform, sometimes emarginate, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary; heads 3.5–3.8 cm wide, including stigmas; inflorescence axes 2–4(–6.7) cm long, quadrangular to slightly flattened, glabrous; bracts calyptra-like, deciduous; peduncles (2.5–5)15–25 mm long. Flowers 5-merous; calyx tubes 2.5–3 mm long, prominently ribbed, glabrous, dilated above the middle, constricted at both ends, lobes 2–2.2 mm long, truncate, prominently ribbed, inside puberulous to tomentose, outside glabrous, toward the base of lobes tomentose; corolla tubes 6–7 × ca. 0.5 mm, glabrous; lobes 3–3.1 mm long, oblong, recurved, ciliate, inside puberulous with a few scattered long hairs around the apex, outside glabrous; anthers ca. 1.5 mm long; filaments ca. 0.5 mm long, glabrous,

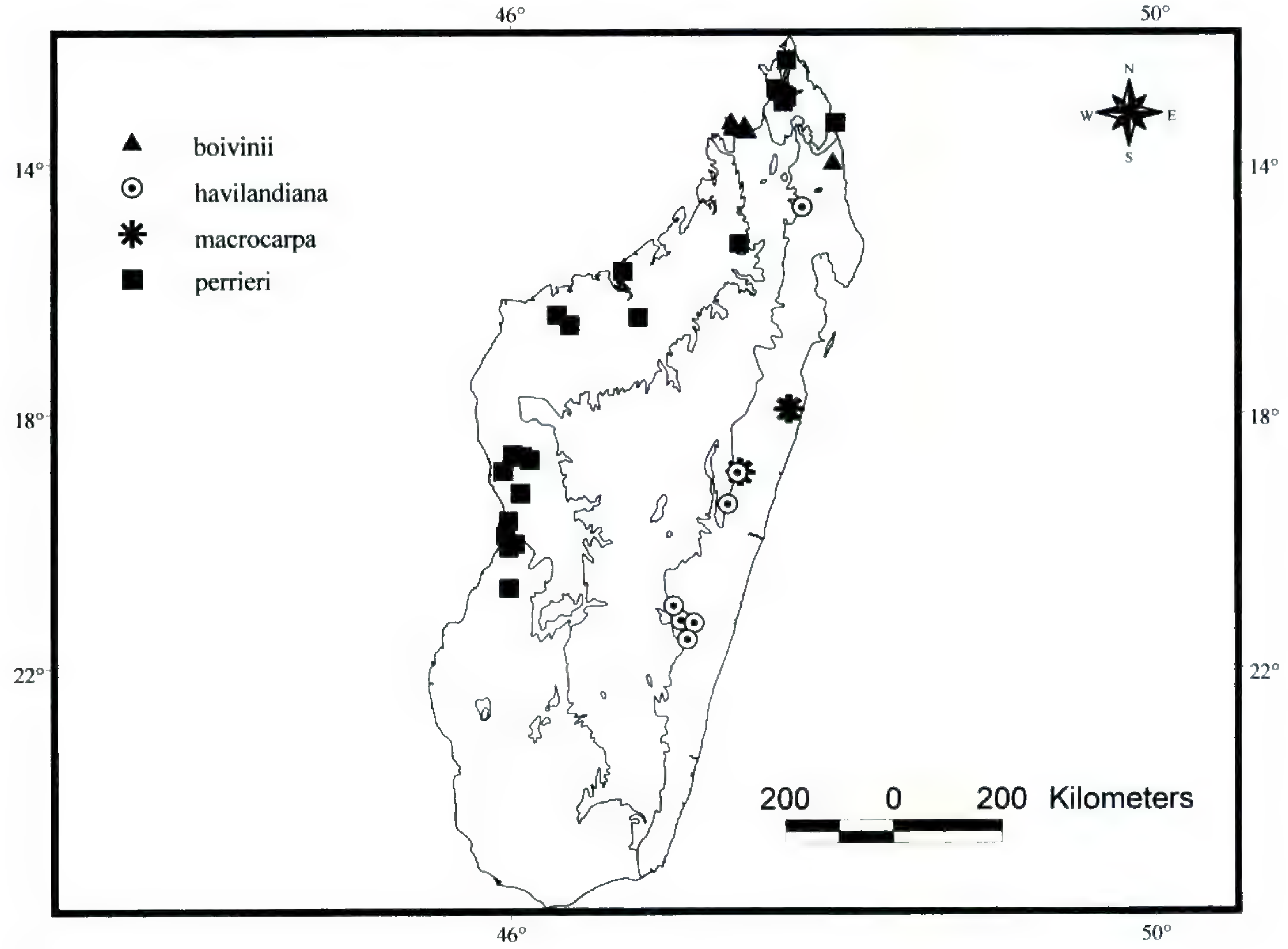

Figure 5. Distribution of *Breonia boivinii*, *B. havilandiana*, *B. macrocarpa*, and *B. perrieri*.

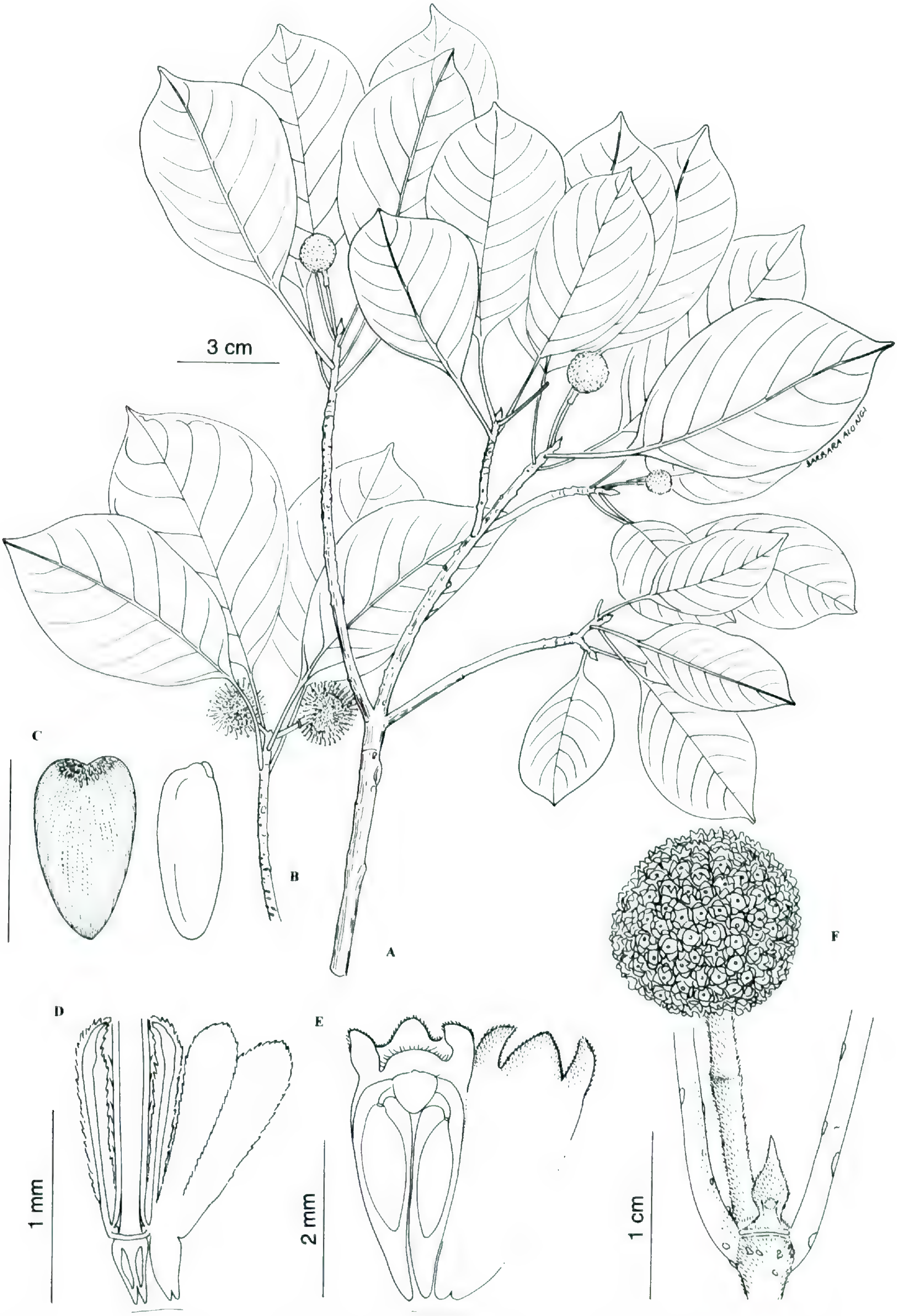

Figure 6. *Breonia capuronii*.—A. Fertile branch with infructescences. —B. Fertile branch with inflorescences. —C. Seed: dorsal view (left); lateral view (right). —D. Two adjacent flowers, showing two adjacent ovaries separated: dissection through corolla and calyx tubes and an ovary of one flower (left); separate flower (right). —E. Median

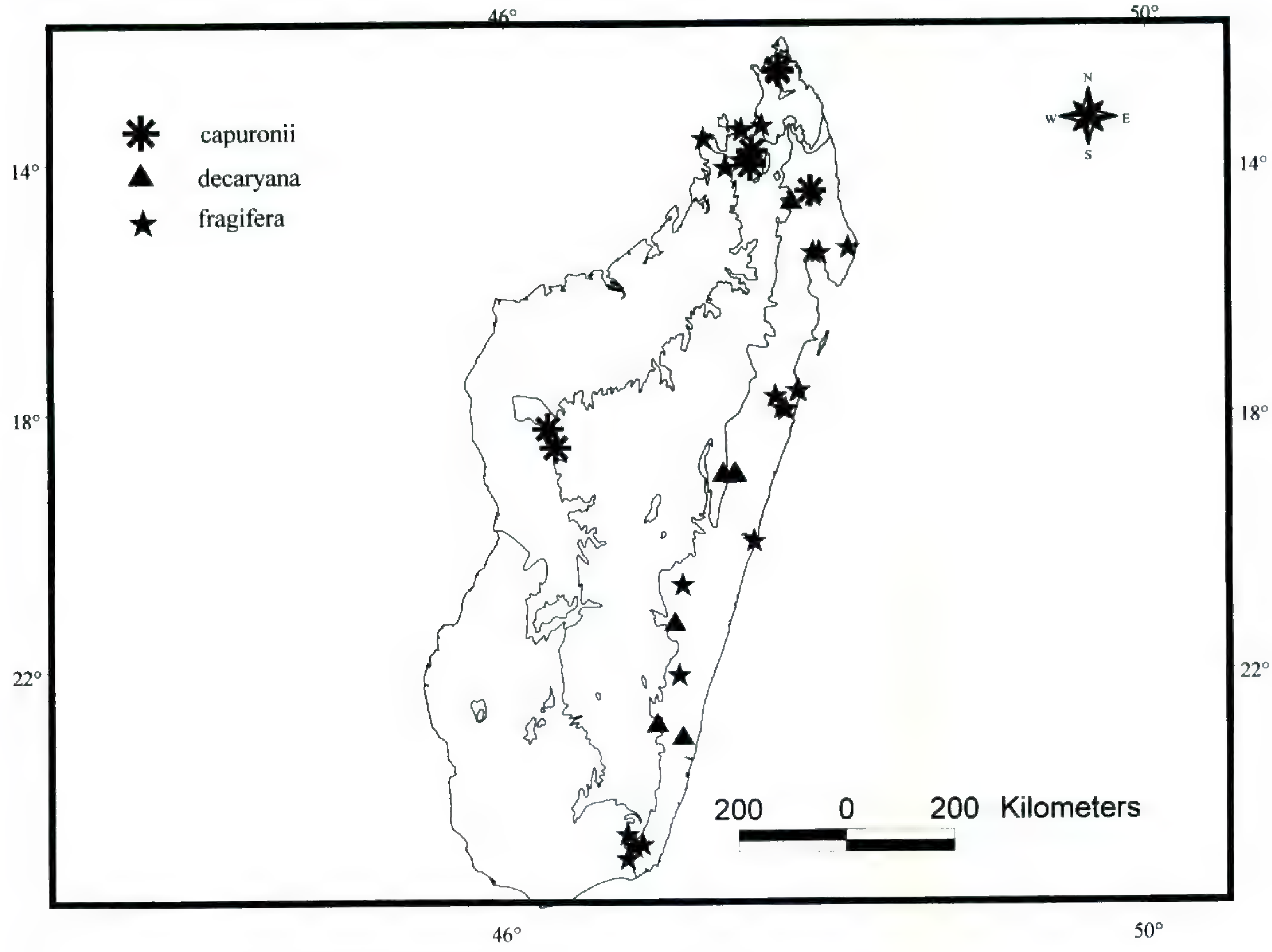

Figure 7. Distribution of *Breonia capuronii*, *B. decaryana*, and *B. fragifera*.

flattened; styles 8–9 mm long, stigmas capitate; ovary 2-carpellate; carpels syncarpous; ovules 6 per locule, pendulous, imbricate; placentae flattened. Infructescences 3–3.5 cm diam., with well-developed calyx remnants; fruits with endocarp soft and fibrous; disks accrescent, obconical; seeds 4 to 6 per locule, strongly flattened, ellipsoid, white-tinged; seed-coat reticulate.

Habitat and distribution. Low- and mid-altitude evergreen rainforests; Districts of Nosy be, Ambanja (Sambirano regions) and Vohémar (Fig. 5).

Common name. Valotro (which is reserved for a particular use).

Phenology. Flowering November to December; fruiting January to February.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Nosy be, Réserve Integrale de Lokobe, *Antilahimena 19* (MO), *Antilahimena 44* (MO), *2751 RN* (P), *Birkinshaw 67* (K, MO, P, TAN); Ankify, *1432 SF* (TEF); Doanilahy, *4905 RN* (TAN), *6234 RN* (TEF); District Ambanja, Presqu'Île d'Ambato, *23424 SF* (TEF), *Randrianaivo 247* (MO), *Ursch s.n.* (P); District Vohémar, Canton Antsirabe-Nord, Forêt d'Analamateza, *27593 SF* (TEF), *27636 SF* (TEF).

2. Breonia capuronii Razafim., sp. nov. TYPE: Madagascar. [Antsiranana province], Massif de Montagne d'Ambre, around "Station forestière des Roussettes," ca. 800–1000 m, 15 Feb. 1962 (fl, young infr.), *22059 SF* (holotype, TEF). Figures 1C and 6.

Haec species ad congeneros nonnullos loculis uniovulatis accedit, sed ab eis petiolo longo (semper 2 cm excedente) atque foliorum nervis secundariis in sicco flavidis distinguitur.

Trees, 15–30 m tall. Bark white-tinged, rugose. Leafy stems terete, puberulous to pubescent, lenticellate. Stipules of terminal vegetative buds conical, 4–5 × 1.5–2 mm, puberulous. Leaves decid-

←

dissection of developed post-anthesal mature flower showing calyx remnant, accrescent disk, and the single seed per locule (left); entire fruit (right). —F. Portion of branch apex with a mature infructescence, a stipule of terminal vegetative bud, and two petioles. A–D from *22059 SF* (TEF) and E, F from *18518 SF* (TEF).

uous; petioles 22–35 × ca. 1 mm, terete, glabrous, lenticellate; blades 9.2–11.5 × 5.3–7.8 cm, broadly elliptic to obovate, clustered near the stem apices, glabrous, membranaceous, glossy, apex acute to mucronate, base rounded; margins glabrous, entire; secondary veins ca. 8 pairs per side, eucamptodromous, adaxially conspicuous, yellow-tinged; domatia absent; stipules ca. 4 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary; heads ca. 2 cm wide; inflorescence axes ca. 1.7 cm long, twisted when dry, terete, densely puberulous; bracts calyptra-like, deciduous; peduncles ca. 1 mm long, densely pubescent. Flowers typically 4-merous; calyx tubes ca. 1 mm long, green-yellow-tinged, inside velutinous, outside pubescent, lobes 0.7–0.9 mm long, triangular, pubescent; corolla tubes 2.8–3.0 × 0.2–0.5 mm, glabrous; lobes ca. 1.5 mm long, oblong, glabrous, toward the apex gradually puberulous, ciliate; anthers ca. 0.5–1 mm long; filaments ca. 0.2 mm long, glabrous, terete; styles 7.8–8 × ca. 0.1 mm, glabrous; stigmas globose or clavate; ovary 2-carpellate; carpels coherent; ovule 1 per locule, pendulous; placentae small, elongated. Infructescences 6–10 mm diam., with persistent calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, obconical; seed 1 per locule, strongly flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Mid-altitude evergreen rainforests and semi-deciduous forests; Districts of Antsiranana II, Ambanja, Sambava, and Tsiroanimandidy (Fig. 7).

Common names. Valodrano (Valotra growing in water), Valotro.

Phenology. Flowering January–February; fruiting March–April.

Discussion. This species is different from the other species of *Breonia* with a single ovule per locule by having long petioles (always more than 2 cm), and secondary leaf veins drying yellow-tinged. It has a large geographical distribution, but appears to be locally rare or perhaps under-collected due to its large size. The type species was collected within the Montagne d'Ambre National Park boundaries.

The specific epithet honors Réné Capuron, a French botanist based in Madagascar for several years in the mid 20th century who worked mainly on Malagasy woody plant families (including Rubiaceae).

Paratypes. MADAGASCAR. **Antananarivo:** District Tsiroanimandidy, Forêt d'Ambohijanahary, *18518 SF* (P, TEF). **Antsiranana:** Montagne d'Ambre National Park, *Malcomber et al. 1219* (MO); District Ambanja, Canton Marovato, Analamateza, *7906 RN* (TEF), *12975 RN* (TEF); Manongarivo, *Gautier* 3772 (G, MO, TAN); District Sambava, Canton Maroambihy, Andranomadiohely, *9002 RN* (TEF).

3. **Breonia chinensis** (Lam.) Capuron, Adansonia, sér. 2, 13: 473. 1973. *Cephalanthus chinensis* Lam., Encycl. Méth. 1: 678. 1785. TYPE: "Isle de France" (Mauritius). [Without exact locality], *Commerson s.n.* (holotype, P-LA photo!). Figures 1D and 2E.

Nauclea citrifolia Poir., in Lam., Encycl. Méth. 4: 435. 1789. *Cephalidium citrifolium* (Poir.) A. Rich., Mém. Fam. Rub. 210. Dec. 1830. *Breonia citrifolia* (Poir.) Ridsdale, Blumea 22: 545. 1975. TYPE: Madagascar. [Without exact locality], *collector unknown s.n.* (holotype, P-LA photo!).

Sarcocephalus richardianus Baill., Adansonia 12: 312. 1879. *Breonia richardiana* (Baill.) Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: Madagascar. [Without exact locality], *Chapelier s.n.* (holotype, P!).

Breonia coriacea Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: Madagascar. [Without exact locality], *Humblot s.n.* (holotype, K!).

Breonia mauritiana Havil., J. Linn. Soc. Bot. 33: 35. 1897. TYPE: Mauritius. [Without exact locality], *Commerson s.n.* (holotype, P!).

Sarcocephalus richardii Drake, in A. Grandidier, Hist. Pl. Madagascar 36: 457. 1897. *Cephalina richardii* Palacky, Cat. Pl. Madagascar 4: 50. 1906. TYPE: *Grandidier* t. *457* (not seen).

Shrubs or trees, 7–25 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Stipules of terminal vegetative buds conical, 5–6 × 1–1.3 mm, glabrous. Leaves persistent; petioles 9–15 × ca. 1 mm, adaxially canaliculate, glabrous; blades 6.4–11 × 2.4–5.5 cm, obovate, glabrous, coriaceous, not glossy, apex broadly to narrowly cuspidate, base cuneate; margins glabrous, entire; secondary veins 8 to 11 pairs per side, eucamptodromous, slightly prominulous; domatia absent; stipules 7–11 × 1.5–2.5 mm, cymbiform, carinate, glabrous, free at the base, deciduous. Inflorescence solitary; heads 1–2.5 cm wide; inflorescence axes 3.4–6.5 cm long, glabrous; bracts calyptra-like, deciduous; peduncles 1–2 mm long. Flowers 5-merous; calyx tubes ca. 1.5 mm long, inside lanate, outside glabrous, pubescent toward the base of the lobes, lobes ca. 0.5 mm long, truncate, lanate; corolla tubes 2.5–5 × 0.5 mm, glabrous; lobes 1.5–2 mm long, oblong, glabrous; anthers 1–1.5 mm long; filaments ca. 0.1 mm long, glabrous, flattened; styles 7.5–9 × 0.3–0.4 mm, glabrous; stigmas clavate to capitate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 3 per locule, pendulous, imbricate; placentae elongated. Infructescences 0.7–2 cm diam., with well-developed persistent calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, ob-

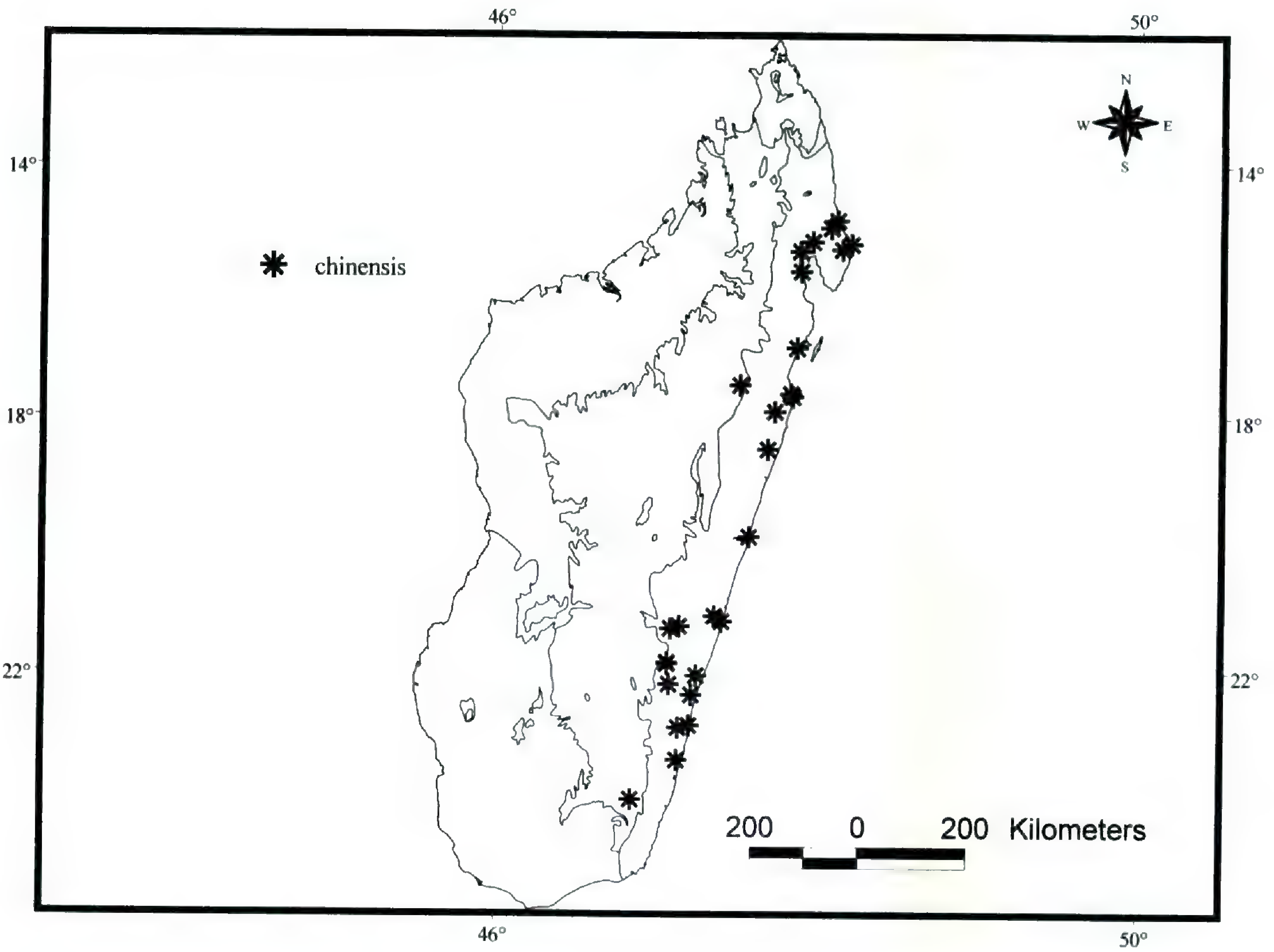

Figure 8. Distribution of *Breonia chinensis.*

conical; seeds 2 to 3 per locule, with rudimentary wings at both ends, strongly flattened, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen rainforests and mid-altitude humid forests, occasionally in dryland sites and riverbeds; Districts of Antalaha, Sambava, Farafangana, Fort-Carnot, Ifanadiana, Manakara, Mananjary, Vangaindrano, Vohipeno, Brickaville, Mahanoro, Maroantsetra, Soanierana Ivongo, and Vavatenina (Fig. 8).

Common names. Molompangady (lips of Valotra), Valopangady (spade of Valotra), Valotra, Valopotsy (white Valotra), Vavalotra, Voakiringy, and Voamalopangady.

Phenology. Flowering August to October; fruiting November to March.

Discussion. *Breonia chinensis* is the most common species of *Breonia* in Madagascar but grows only in evergreen rainforests. The epithet "*chinensis*" is not the most appropriate choice for *Breonia,* which is restricted to Madagascar; however, it has priority over the other available basionyms. Candidate basionyms of *B. chinensis* were all considered separate species of *Breonia* until Capuron (1973a), endorsed by Bosser (1984, 1999), clarified the identity of *Cephalanthus chinensis* Lam. as a separate species of *Breonia.* Homolle (1938) reduced *Breonia coriacea* Havil. to synonymy under *B. richardiana* Havil. *Breonia coriacea* was not mentioned by Ridsdale (1975), but both species definitely belong to *Breonia chinensis* based on their leaf blade shape and size, inflorescence axis shape, and ovule number.

It has been accepted that the original description of *Nauclea citrifolia* Poir. [= *B. chinensis*] is in Lamarck's *Encyclopédie* (1789: 435) and that this species belongs to *Breonia* (Bakhuizen van den Brink, 1970; Ridsdale, 1975; Bosser, 1984, 1999). However, Poiret did not specify type specimens of any of his species. This has caused some confusion as to which specimen he based *N. citrifolia* on and led to disagreement over the identity of the name. Richard (1830: 219) stated that his *Cephalidium citrifolium* (Poir.) A. Rich. was a new combination based on *N. citrifolia* Poir.: "*Nauclea sp.* Poir., Encycl. méth., . . . Species unica observata: *Cephalidium citrifolium,* Nob. (*Nauclea citrifolia,* Poiret, l. c.)." Like Poiret, Richard also did not cite the type specimens of any of his species.

There is one specimen (lacking the collector's

name and number) with four labels in P-LA that may be the type of *N. citrifolia* Poir. The first label is Lamarck's and says: "*Nauclea citrifolia* dic n° 2." The second is Roeper's and states: "? 8. *Nauclea cadamba* Roxb.? [and] *Nauclea citrifolia* Poir.!!!, *perquem affinis orientalis!* immonimis affinis." The third states that this specimen returned to P-LA: Herbier de Lamarck, "acquis en Novembre 1886." The fourth label is that of Capuron and states: "*Breonia chinensis* (Lamk.) R. Capuron." Capuron (1973a) considered that this Lamarck specimen is the type of *Nauclea citrifolia* Poir. and is conspecific with *Breonia chinensis* (Lam.) Capuron. I concur with him because the protologue of *N. citrifolia* Poir. in Lamarck (1789: 435) agrees with this specimen. Ridsdale (1975) also endorsed Capuron's view, but made the new combination *Breonia citrifolia* (Poir.) Ridsdale because he did not recognize *Cephalanthus chinensis* Lam. as a *Breonia*. Noteworthy is that Ridsdale did not cite the type specimen of *N. citrifolia* Poir. Bosser (1984) disagreed with Capuron, arguing that an unnumbered Commerson collection from Madagascar in P-LA is the type specimen of *N. citrifolia* Poir. It is unclear whether Bosser referred to the *Commerson s.n.* in P-LA that serves as the type of *Cephalanthus chinensis* Lam. In any case, this does not correspond to the protologue of *N. citrifolia* Poir.

Despite Richard's statement (Richard, 1830: 210) that his *Cephalidium citrifolium* [= *Breonia chinensis*] was based on *Nauclea citrifolia* Poir., Bosser (1984) argued that the name *Cephalidium* was not based on the same type as *N. citrifolia* and therefore should be cited as *Cephalidium citrifolium* A. Rich. Also, Bosser further argued that the type specimen of *C. citrifolium* is another unnumbered collection of Commerson now in P. This *Commerson s.n.* at P collection is misidentified as *N. citrifolia* Poir., but it is actually a completely different species of *Breonia* I describe here as *B. taolagnaroensis*. This P collection of Commerson has fruit only, whereas both Poiret's protologue of *N. citrifolia* and Richard's protologue of *Cephalidium citrifolium* included flowers and fruits. Ridsdale (1975) treated *Cephalidium citrifolium* (Poir.) A. Richard under his *Breonia citrifolia* (Poir.) Ridsdale, but I here consider it as a synonym of *Breonia chinensis* (Lam.) Capuron.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antalaha, Soahitra, "suivant le ruisseau Soahitra dans la vallée," *s.n. SF* (TEF); Ambohitralanana, *9982 RN* (TEF); Andrakarana, *9238 SF* (TEF); Maromandia, Forêt de Bero, *12447 SF* (TEF); Ambodiazovola, Ampanavoana, Vinanivao, Forêt de Sahaenjika, *Bernard 327* (MO, TAN); Canton Antafononana, Vinanivao, Ampanavoana, Parc Masoala, *Bernard 187* (MO, TAN); District Sambava, Canton Analamanara au Sud de Tsaratanana, between Sambava and Antsirabe-Nord, *27192 SF* (TEF); [Unknown locality], *Vigreuse 15418* (TAN). **Fianarantsoa:** District Farafangana, Karianga, *Decary 5511* (PRE), *Decary 5513* (P), *Decary 5573* (PRE); Efatsy, Forêt d'Analazaha, *15381 SF* (TEF); Canton Ivato, Forêt d'Analila, *16217 SF* (TEF), *15495 SF* (TEF); District Fort-Carnot, Canton Ifanirea, Forêt d'Analamarina, *15287 SF* (TEF); Canton Tolongoina, Ambinanindrano, *5964 SF* (TEF); Ambatomalama, *15518 SF* (TEF); Canton Manampatrana, "exploitation forestière" Ahamode Ionilahy, *7155 SF* (TEF); District Ifanadiana, Ranomafana National Park, between Morafeno and Sahavanana, *Turk et al. 643* (MO, TAN); Canton Kianjavato, entre Ifanadiana et Anosivolo, *23917 SF* (TEF); District Manakara, Forêt d'Andafa, *14728 SF* (TEF); Forêt de Manakara au nord du terrain d'aviation, *86-R-118* (TEF); District Vohipeno, vestiges de forêt au Nord de Vohipeno, *23691 SF* (TEF); Tsararano, *6360 SF* (TEF); District Mananjary, Canton Anosimparihy, Manakana, *14437 SF* (TEF); Canton Morafeno, Ambodinonoka, *16174 SF* (TEF); Marofototra, Forêt de Mananjavara, *14712 SF* (TEF); District Vaingaindrano, between Lopary and Vangaindrano, *23661 SF* (TEF). **Toamasina:** District Brickaville, Managisy, *12352 SF* (TEF); District Mahanoro, Canton d'Ambodinanidilana 1 km à l'Est d'Ambodiala, Forêt d'Amboagibe, *19658 SF* (TEF); remnant native vegetation 1–2 km E of Fampanambo, *Schatz et al. 3858* (MO, TAN); District Maroantsetra, Canton Andranofoy, Ambodikakazo au bord de la rivière d'Andranofotsy, *21596 SF* (TEF); Baie d'Antongil, bassin de Rantabe, between Antsambalahy and Beanana, *9047 SF* (TEF); Masoala National Park, Andrombazaha, *Rahajasoa et al. 747* (MO); District Soanierana Ivongo, *2410 SF* (TEF); Toamasina II, Canton Ampan'Onive, Andranotsara, Mahatsara, *33240 SF* (TEF), *34711 SF* (TEF), *34719 SF* (TEF); Ambodiriana, *17299 SF* (TEF); Vohimarangitra, *31809* (TEF); Forêt d'Analalava à l'Ouest de Foulpointe, *28081 SF* (TEF); District Vavatenina, Canton Sahatavy, Maizinandro, *26103 SF* (TEF).

4. **Breonia cuspidata** (Baker) Haviland, J. Linn. Soc. Bot. 33: 37. 1897. *Nauclea cuspidata* Baker, J. Linn. Soc. Bot. 25: 319. 1890. TYPE: Madagascar. "North West" [without exact locality], Sep. 1887 (fl), *Baron 5563* (holotype, K!).

Trees, height unknown. Bark with annular fissures. Leafy stems rounded, glabrous. Terminal vegetative buds conical, 4–5 × 1–1.2 mm, glabrous. Leaves persistent; petioles ca. 10–13 mm long, adaxially canaliculate, glabrous; blades 5.5–10 × 1.9–3 cm, oblanceolate, glabrous, membranaceous, glossy, apex caudate, base attenuate; margins glabrous, entire; secondary veins 8 to 9 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules ca. 5 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 4.5–6.5 cm long, strongly flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles not present. Flowers 5-merous; calyx tubes ca. 1

mm long, free, inside lanate, outside up to the middle glabrous, above the middle lanate; lobes ca. 0.2 mm long, triangular, lanate; corolla tubes ca. 5 × 0.8–0.9 mm; lobes 1.1–1.3 mm long, broadly oblong, glabrous; anthers 0.7–0.8 mm long, filaments 0.2–0.3 mm long; styles 8–9 mm long; stigmas clavate to capitate; ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae reduced, pendulous. Infructescences not seen.

Distribution and habitat. Northwest Madagascar; habitats unknown.

Common names. Unknown.

Phenology. Flowering September; fruiting time unknown.

Discussion. *Breonia cuspidata* appears to have a restricted distribution and has not been collected since 1890. This species is distinguished from the other species by its ovaries with one ovule per locule and its leaf blades with caudate apices and attenuate bases.

Original paratypes. [Unknown locality], *Baron 6602* (K!) and *Scott Elliott 2214* (K!).

5. Breonia decaryana Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. *Neobreonia decaryana* (Homolle) Ridsdale, Blumea 22: 546. 1975. TYPE: Madagascar. [Fianarantsoa province], District Farafangana, Ifandana, *Decary 5199* (holotype, P!; isotype, L not seen). Figures 1A and 2A.

Breonia keliravina Homolle, Bull. Soc. Bot. France 84: 460. 1937 [publ. 1938]. TYPE: Madagascar. Analamazaotra, *Thouvenot 91* (lectotype, designated by Ridsdale (1975: 546), P!).

Trees, 10–30 m tall. Bark rugose with annular fissures, rarely smooth, lenticellate. Leafy stems quadrangular, glabrous, always dichotomously branched. Terminal vegetative buds complanate, 8–14 × 6–10 mm, glabrous. Leaves persistent; petioles 10–20 × 2–3 mm, adaxially canaliculate, glabrous; leaf blades (4–)6.5–12 × (1.5–)3–7.5 cm, oblanceolate to broadly obovate or broadly elliptic, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate to attenuate, or rounded; margins glabrous, entire; secondary veins (6 or 7) to 10 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules 10–14 mm long, ovate to obovate, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences 4 to 8 per axil; heads 1.5–1.8 cm wide; inflorescence axes 2.8–5 cm long, terete or slightly flattened; bracts calyptra-like, persistent; peduncles 0.8–2 cm long, sparsely pubescent. Flowers 4-merous; calyx tubes ca. 1 mm long, completely fused, lobes ca. 1 mm long, inside and outside densely pubescent; corolla tubes ca. 4 × 1 mm, red, glabrous, lobes ca. 1 mm long, broadly oblong, yellow-tinged, glabrous; anthers ca. 1 mm long. Styles 7–8 × 1–1.5 mm; stigmas globose; ovary 2-carpellate; carpel coherent; ovule 1 per locule, pendulous; placentae small. Infructescences 0.5–1.7 cm diam., rugose, with calyx remnants barely evident; individual fruits with endocarp hard, glossy; disks accrescent, rounded, deeply divided; seed 1 per locule, strongly flattened, red; seed-coat lineate.

Habitat and distribution. Evergreen rainforests, occasionally in riverbeds; Districts of Andapa, Moramanga, and Farafangana (Fig. 7).

Common names. Molompangady keliravina, Marotsaka, Valompangady, Valotro, and Valotsy.

Phenology. Flowering May to August; fruiting September to February.

Discussion. *Breonia decaryana* can easily be distinguished from the rest of the *Breonia* species by its complanate terminal vegetative buds and 4 to 8 inflorescences per axil. This species was removed by Ridsdale from *Breonia* simply because it has flattened terminal vegetative buds and partly fused corolla tubes. I here include it in *Breonia* because this species shares one morphological synapomorphy with *Breonia* sensu Ridsdale (large accrescent disks); additionally, they all have multiple fruits. I endorsed Ridsdale's decision on sinking *B. keliravina* in *B. decaryana* because the former has all the diagnostic features of the latter. The specimen *Louvel 216* (P!) was one of the two cited by Homolle (1938) in the protologue of *B. keliravina*.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Andapa, Réserve Spéciale d'Anjanaharibe-Sud, *Razafimandimbison SG 257* (MO, TAN). **Toamasina:** District Moramanga, Canton Analamazaotra, *Thouvenot s.n.* (P), *Louvel 216* (P); Ambodivoasary, *12-B-R-172* (TEF); Anosibe, *26804 SF* (TEF), *28414 SF* (TEF), *28445 SF* (TEF).

6. Breonia fragifera Capuron ex Razafim., sp. nov. TYPE: Madagascar. Antsiranana province: District Antalaha, Canton Ampanavoana, Antsiramoranga, 6 Dec. 1954 (fl), *6809 RN* (holotype, TEF). Figures 2C and 9.

Haec species a congeneris disco nectarifero accrescente permagno atque fructu pustulato distinguitur.

Shrubs, spreading shrubs, or trees, 5–15 m tall. Bark rugose. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3–3.5 × ca. 3 mm, glabrous. Leaves persistent; petioles 25–70 × ca. 1.5 mm, terete, glabrous; blades 8–13 × 2.2–4(–6.5)

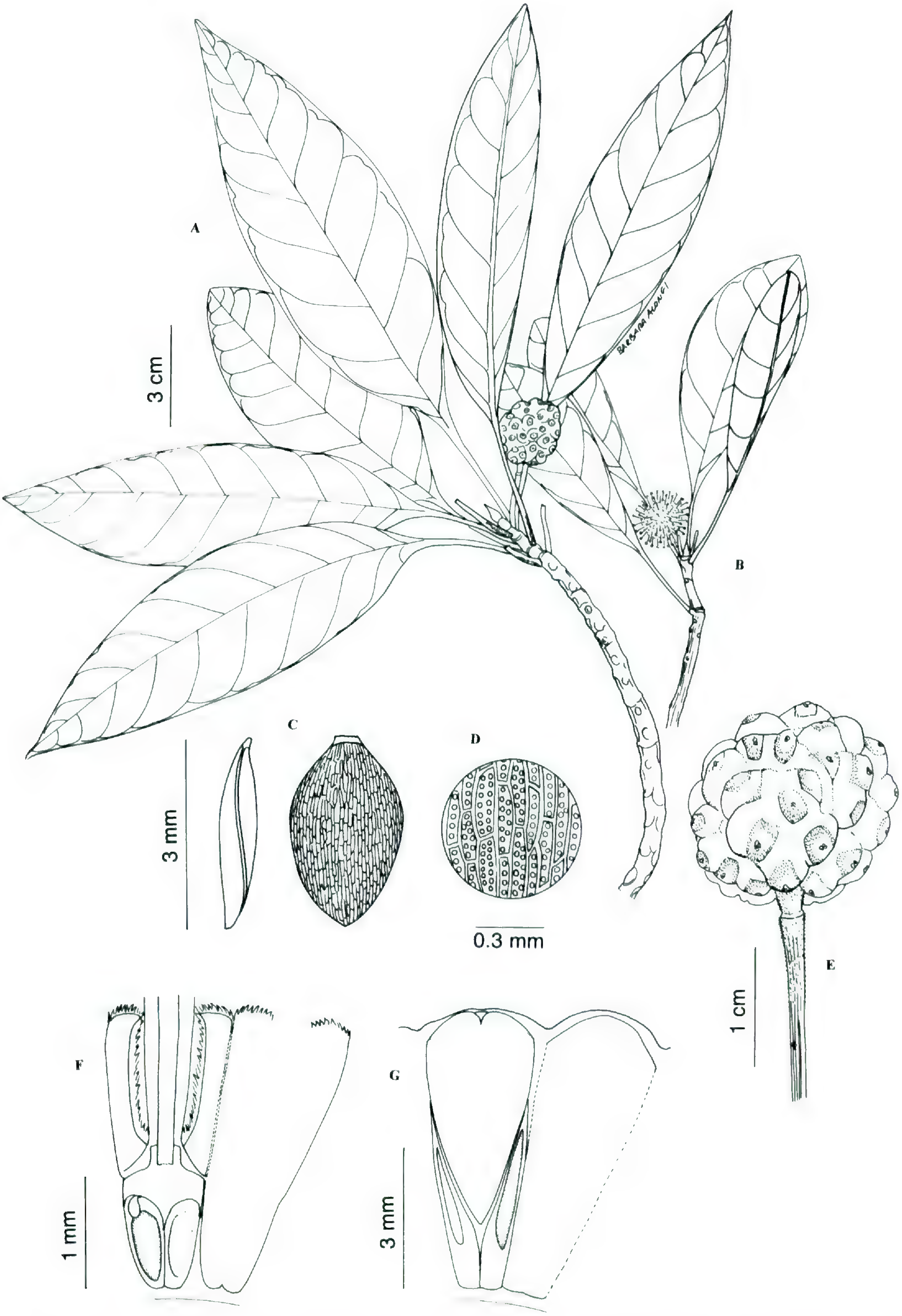

Figure 9. *Breonia fragifera.*—A. Fertile branch with mature infructescence. —B. Fertile branch with inflorescence. —C. Seed, showing flattened lateral profile (left); dorsal view (right). —D. Seed-coat texture. —E. Mature infructescence. —F. Median dissection through flower, showing velutinous calyx tube and unicarpellate ovary with single pen-

cm, oblanceolate to ovate, glabrous, coriaceous or membranaceous, glossy, apex cuspidate to acute, base cuneate; margin glabrous, entire; secondary veins 7 to 9 pairs per side, eucamptodromous; domatia absent; stipules ca. 3 × 2 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary; heads 1.5–2 cm wide; inflorescence axes 1.2–3.5 cm long, terete; bracts calyptra-like, deciduous; peduncles 2–3 mm long. Flowers mostly 4-merous; calyx tubes ca. 0.5 mm long, velutinous, lobes lanate; corolla tubes ca. 4 × 1 mm, white-tinged, glabrous; lobes ca. 1 mm long, oblong, ciliate or glabrous; anthers ca. 0.5 mm long; filaments ca. 0.1 mm long, glabrous, terete; styles ca. 7 × 0.2 mm, glabrous; stigmas capitate; ovary 2-carpellate; carpels coherent; ovules 1 per locule, pendulous. Infructescences 1.6–2 cm diam., pusticulate, with calyx remnant barely evident; individual fruits with endocarp soft, fibrous; disks accrescent, massive, obtriangular; seed 1 per locule, strongly flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Low-altitude forests; Districts of Ambanja, Antalaha, Fort-Carnot, Toamasina II, Fort-Dauphin (Fig. 7).

Common names. Valotra, Valotralahy (male Valotra).

Phenology. Flowering November–March; fruiting June to March.

Discussion. This species is diagnosed by its massive, accrescent disks and pusticulate fruits. It was lumped by Ridsdale (1975) in *Breonia sphaerantha.* The species name was taken from the labels of the herbarium specimens of *Breonia fragifera* received from TEF. The epithet "*fragifera*" indicates strawberries-bearing, referring to its inflorescences.

Paratypes. MADAGASCAR. **Antsiranana:** District Ambanja, *Randrianaivo 251* (MO); Beampangibe, *2961 SF* (TEF); Besinkara, Ambalafary, *Gautier et al. 3288* (K, MO); Canton Marovato, Mahalina, *7460 SF* (TEF); Presqu'Île d'Ambato, forêt classée, *Antilahimena et al. 324* (MO); District Antalaha, Canton Ampahana, Andranomadio, *21570 SF* (TEF). **Fianarantsoa:** District Fort-Carnot, Canton Ifanirea, *19791 SF* (TEF), *19775 SF* (TEF). **Toamasina:** Ambodiriana *9045 RN* (TEF); environs de la Baie d'Antongil, Massif d'Antsirosiro, *8734 SF* (TEF); Toamasina II, Ampasimbe, Andranotsara, SFF Mahatsara, *Comtet 33237 SF* (TEF), *Comtet 33536 SF* (TEF), *Comtet 34288 SF* (TEF), *Comtet 34413 SF* (TEF), *Noyes et al. 961* (K, MO, P, TAN); Réserve Naturelle Intégrale de Betampona, piste Sahafoza, *Andrianarisata et al. 259* (TAN). **Toliara:** District Fort-Dauphin, *5152 RN* (P, TEF), *Randriamampionona 438* (MO); Canton Ifarantsa, Antsako, *10803 SF* (TEF); Isaka-Ivondro au bords de la rivière Kovazaza, *11503 SF* (TEF).

7. Breonia havilandiana Homolle, Bull. Soc. Bot. Fr. 84: 464. 1937 [publ. 1938]. TYPE: Madagascar. [Fianarantsoa province], "bords de l'Anosivola (Mangoro)," 700 m, Sep. 1911 (fl), *Perrier de la Bâthie 3904* (holotype, P!).

Trees, 10–20 m tall. Bark fissured longitudinally. Leafy stems glabrous, lenticellate. Terminal vegetative buds conical, 15–19 × 3.5–4 mm, glabrous. Leaves deciduous; petioles 15–25 × ca. 2 mm, terete, glabrous; blades 8–19(–21) × 5–9(–12) cm, obovate, always rippled or wavy when dry, glabrous, coriaceous, apex obtuse to rounded, base cuneate; margins glabrous, entire; secondary veins 8 to 10 pairs per side, eucamptodromous, abaxially prominent; ciliate-type domatia; stipules ca. 20 × 3 mm, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescence solitary, rarely 2 per axil, heads ca. 2.3–2.9 cm wide; bracts calyptra-like; inflorescence axes 3–4 cm long, glabrous; peduncles ca. 3–4 mm long, glabrous. Flowers 5-merous; calyx tubes ca. 3.5 mm long, inside at the base velutinous, toward the lobes pubescent, outside glabrous, a few straight long hairs surrounding the base, lobes oblong, tomentose; corolla tubes ca. 5 × 0.6–0.7 mm, glabrous, lobes 15–2.5 mm long, oblong; anthers 1.1–1.2 mm long; filaments ca. 0.1 mm long, glabrous, flattened; styles 8.5–9 × ca. 0.2 mm, glabrous; stigmas capitate, shallowly bifid; ovary 2-carpellate; carpels syncarpous; ovules 2 to 4 per locule, flattened, pendulous, imbricate; placentae flattened, elongated. Infructescence 1.7–2.5 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, not glossy; disks accrescent, obconical; seeds 2 to 4 per locule, strongly flattened, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Low- and mid-altitude evergreen rainforests; Districts of Ifanadiana, Befandriana-Nord, Moramanga, Fort-Carnot, and Anosibe an'Ala (Fig. 5).

Common names. Molompangady, Molotr'angady (lips of spade), Mamalifangady.

Phenology. Flowering October to November; fruiting September to January.

Discussion. This species is distinctive in having leaf blades that are undulate when dry.

Additional specimens examined. MADAGASCAR.

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dulous ovule each (left); entire flower (right). —G. Median dissection through infructescence revealing massive disk and uniovulate carpels (left); entire fruit (right). A, B, F from *6809 RN* (TEF) and C–E, G from *19775 SF* (TEF).

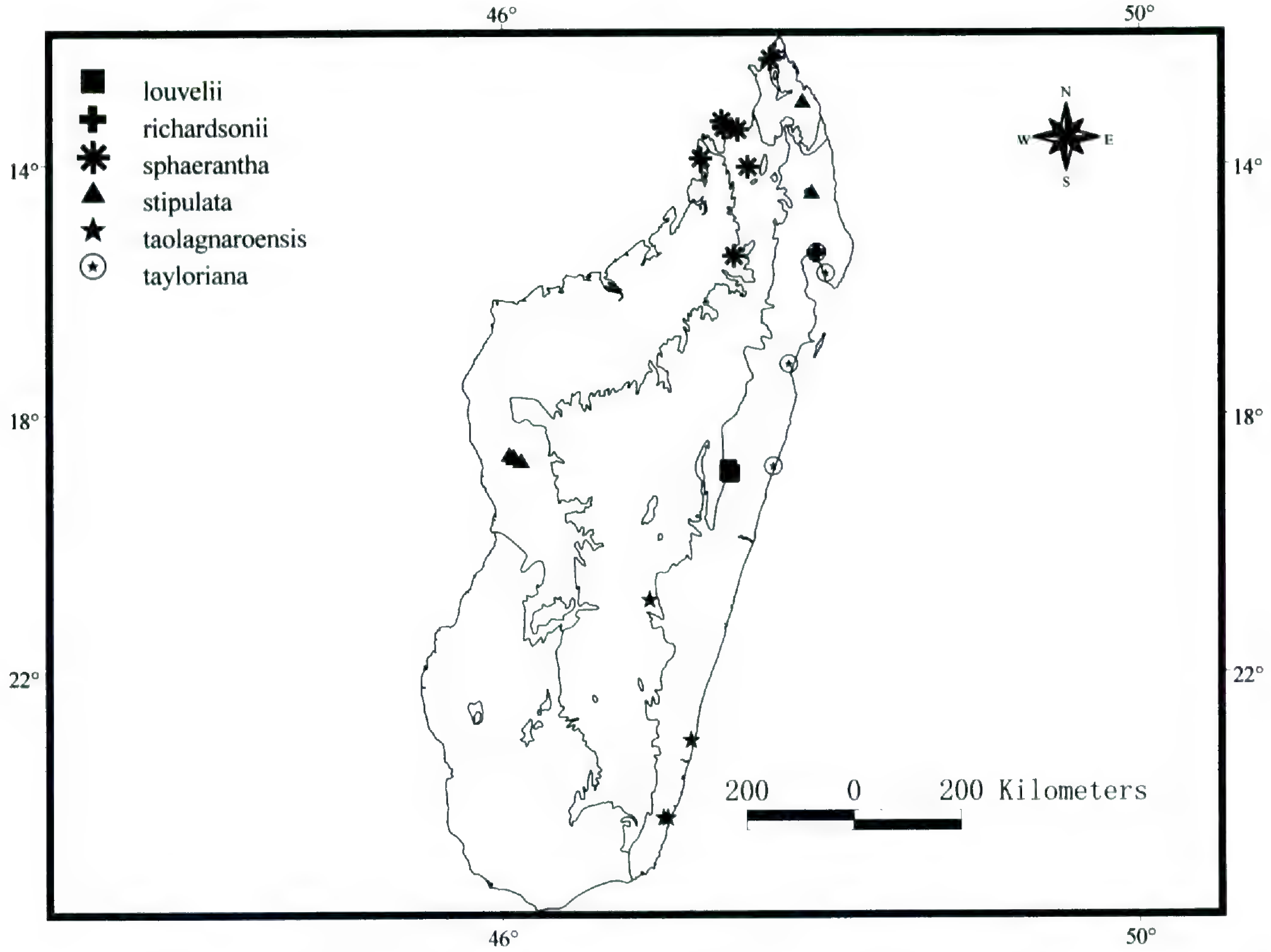

Figure 10. Distribution of *Breonia louvelii*, *B. richardsonii*, *B. sphaerantha*, *B. stipulata*, *B. taolagnaroensis*, and *B. tayloriana*.

Fianarantsoa: District Fort-Carnot, Canton Tolongoina, Ankadilalana, *19295 SF* (TEF); Forêt d'Ambatoharanana, *7136 SF* (TEF); District Ifanadiana, Ranomafana National Park, *Randrianasolo & Rasabotsy 32* (MO), *9974 SF* (TEF), *Razafimandimbison SG 389* (MO, TAN). **Mahajanga:** District Befandriana-Nord, Canton Matsondakana, Belalona, Réserve Spéciale d'Anjanaharibe-Sud, *Ravelonarivo & Rabesaonina 570* (MO). **Toamasina:** District Anosibe an'Ala, Tsaratampona, Mangorobilika, *25526 SF* (TEF); District Moramanga, Canton Périnet, Sahamaloto, *6105 SF* (TEF).

8. Breonia louvelii Homolle, Bull. Soc. Bot. France 84: 461. 1937 [publ. 1938]. TYPE: Madagascar. [Toamasina province], Analamazaotra, Sep. 1925 (fl), *Louvel 125* (holotype, P!).

Medium-sized trees, 7–10 m tall. Bark with longitudinal fissures. Leafy stems rounded, glabrous, lenticellate. Terminal vegetative buds conical, 5–9 × 1–1.5 mm long, glabrous. Leaves persistent; petioles ca. 7–17 mm long, adaxially canaliculate, glabrous; blades ca. 4–9 × 1.5–3.5 cm, oblanceolate to elliptic, glabrous, coriaceous, glossy, apex acuminate to obtuse, base attenuate; margins glabrous, entire, slightly involute when dry; secondary veins 10 to 11 pairs per side, eucamptodromous, adaxially inconspicuous, abaxially conspicuous; domatia absent; stipules 5–9 × 1.5–1.8 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 1.8–2 cm wide; inflorescence axes 2–4 cm long, flattened, slender, glabrous; bracts calyptra-like, deciduous; peduncles ca. 2 mm long, glabrous. Flowers 5-merous or rarely 6-merous; calyx tubes ca. 1 mm long, free, lobes ca. 1 mm long, inside lanate, outside glabrous, lobes densely pubescent, truncate to oblong; corolla tubes 5–6 × 1–1.2 mm, glabrous, lobes 2–3 mm long, broadly oblong; anthers 1–1.5 mm long; filaments 0.2–0.3 mm long; styles 7–8 × 1–1.5 mm; stigmas capitate (shallowly bifid); ovary 2-carpellate; carpels syncarpous; ovule 1 per locule, pendulous; placentae small. Infructescences not seen.

Habitat and distribution. Evergreen rainforests; District of Moramanga (Fig. 10).

Common names. Hazomarotsaka (slender but tall trees), Molompangady.

Phenology. Flowering September to October; fruiting December to January.

Discussion. This species has a very restricted geographical distribution and appears to be rare.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Moramanga, Canton Périnet, Antaniditra, *7921 SF* (TEF); Sahamaloto, *7562 SF* (TEF); Réserve Spéciale d'Analamazaotra, *Razafimandimbison SG 358* (MO, TAN).

9. Breonia lowryi Razafim., sp. nov. TYPE: Madagascar. Fianarantsoa province: Ambalavao, Andringitra Reserve, *Lewis et al. 755* (holotype, MO 05066234; isotypes, K, TAN). Figure 11.

Haec species a congeneris loculis corollinis glabris, tubo calycino intus glabro atque loculis 7- ad 9-ovulatis distinguitur.

Trees, 10–30 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds ca. 3 × 2 mm, glabrous. Leaves persistent, petioles 10–14 mm long, adaxially canaliculate, glabrous; blades (5.5–)7.8–12 × (2.4–)3.4–6.4 cm, obovate, glabrous, coriaceous, not glossy, apex broadly cuspidate, base attenuate; margins glabrous, entire; secondary veins 6 to 9 pairs per side, eucamptodromous, abaxially conspicuous; pit-type domatia in the axils of the secondary veins, pubescent; stipules ca. 5 × 1–1.2 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2–2.3 cm wide; inflorescence axes ca. 1.8–3 cm long, flattened, glabrous; bracts calyptra-like, deciduous; peduncles ca. 2 mm long, glabrous. Flowers 5-merous; calyx tubes ca. 2 mm long, inside glabrous, outside puberulent, lobes 0.5–0.8 mm long, oblong, inside glabrous, outside velutinous; corolla tubes ca. 6 × 0.4 mm, reddish, inside puberulous, outside glabrous, lobes 2–2.2 mm long, oblong, puberulous; margins glabrous; anthers 0.5–0.8 mm long; filaments ca. 0.2 mm long, flattened; styles ca. 8 × 0.6 mm; stigmas elongate to capitate; ovary 2-carpellate; carpels syncarpous; ovules 7 to 9 per locule, pendulous; placentae elongated. Infructescence 1.1–1.5 cm diam., with well-developed calyx remnants; individual fruits berry-like; endocarp soft, fibrous; disks accrescent, rounded; seeds 7 to 9 per locule, strongly flattened, with rudimentary wings, red; seed-coat reticulate.

Habitat and distribution. Evergreen forests between 900 and 1500 m altitude; Districts of Fort-Carnot, Moramanga, Ambalavao, and Fianarantsoa (Fig. 12).

Common names. Molompangady, Valompangady.

Phenology. Flowering time unknown; fruiting May and October.

Discussion. This species differs from the other *Breonia* species that also have 7 to 9 ovules per locule and glabrous corolla lobes because the inside of the calyx tubes is glabrous. The epithet of this new name honors Porter P. Lowry II, head of the Africa and Madagascar Department of the Missouri Botanical Garden, who has done much to further studies of the Araliaceae as well as other plant families in Madagascar.

Paratypes. MADAGASCAR. **Fianarantsoa:** District Fianarantsoa II, Canton Ampamaherana, *2078 SF* (TEF); District Fort-Carnot, Canton Tolongoina, Andrambovato, *9711 SF* (TEF), *11594 SF* (TEF), *14-B-R-230* (TEF). **Toamasina:** District Moramanga, Forêt d'Analamazaotra (Périnet), *24150 SF* (TEF).

10. Breonia macrocarpa Homolle, Bull. Soc. Bot. Fr. 84: 461. 1937 [publ. 1938]. TYPE: "Madagascar," *Périer de la Bâthie 3933* (lectotype, designated by Ridsdale (1975: 545), P!). Figures 2D and 3D.

Trees, 10–20 m tall. Bark longitudinally fissured. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 27–40 × 4–6 mm, puberulent. Leaves persistent; petioles 35–60 × ca. 4 mm, terete, lenticellate, puberulous; blades 19.5–38 × 15–25 cm, broadly ovate to broadly oblanceolate, brown-tinged when dry, adaxially glabrous, abaxially sericeous, coriaceous, glossy, apex cuspidate to rounded, base rounded; margins glabrous, entire; secondary veins 12 or 13 pairs per side, eucamptodromous, abaxially densely pubescent, adaxially glabrous; tuft-domatia in the axils of secondary and tertiary veins; stipules 27–34 × 6–9.5 mm, cymbiform, abaxially carinate, puberulous, free at the base, deciduous. Inflorescences solitary, heads ca. 4.7 cm wide; inflorescence axes 8.5–12.5 cm, flattened, glabrous to puberulous; bracts calyptra-like, deciduous; peduncles not elongated. Flowers 5-merous or rarely 4-merous; calyx tubes 2.8–3 mm long, green, below the middle velutinous, around the mid-part glabrous, toward the lobes puberulous; lobes ca. 2 mm long, truncate to oblong, velutinous; corolla tubes ca. 11 mm long, glabrous, lobes ca. 3.5 × 0.25 mm long, oblong, glabrous, puberulous toward the apices; margins ciliate; anthers ca. 2 mm long; filaments 0.5–1 mm long, flattened. Styles ca. 21 × 0.5 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 4 to 6 per locule, flattened, pendulous, imbricate; placentae strongly flattened, elongated, adnate to the septum. Infructescences 3–4 cm diam., woody when dry, with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, pentagonal; seeds 4 to 6 per locule, strongly flattened, ellipsoid, red, reticulate.

Phenology. Flowering March to May, August to

September; fruiting May to July, December to January.

Habitat and distribution. Low- and mid-altitude of eastern evergreen rainforests; Districts of Brickaville, Moramanga, and Toamasina II (Fig. 5).

Common names. Molompangady and Valotra.

Discussion. Ridsdale (1975: 545) included *Breonia macrocarpa* as a synonym of *B. madagascariensis*, dismissing the former as "a hairy-leaved form" of the latter. However, these two are quite different morphologically, as is clear from Table 3. Despite the striking morphological differences between the two species, *B. macrocarpa* has not been recognized since its original description, partly because Homolle (1938) did not provide keys for the species of *Breonia* she recognized and partly because no collections of *B. madagascariensis* have been made for almost 200 years.

While describing this species, Homolle cited three specimens, *Thouvenot 117* (P!), *Perrier de Bâthie 3933* (P!), and *Perrier de la Bâthie 5270* (P!), without selecting the type species.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Brickaville, Fetromby, Ambalakondro, *3265 SF* (TEF); District Moramanga, Perinét, *26906 SF* (TAN), *Noyes et al. 974* (K, MO, P, TAN), *Razafimandimbison SG 352* (MO, P, TAN); District Toamasina II, Canton Ambodiriana, Vohimarangitra, *9052 RN* (P), *9129 RN* (P); Canton Ambodiriana, *18116 SF* (P, TEF), *21160 SF* (TEF), *28136 SF* (TEF), *32344 SF* (TEF).

11. Breonia madagascariensis A. Rich., in DC., Prodr. 4: 620. Sep. 1830. *Sarcocephalus madagascariensis* (A. Rich.) Baill., Adansonia 12: 311. 1879. TYPE: "Madagascar." [Without exact locality], *Chapelier s.n.* (lectotype, designated by Ridsdale (1975: 545), K!; isolectotype, P!). Figure 1F.

Trees, height unknown. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, ca. 35 × 6 mm, glabrous. Leaves persistent, subsessile; blades ca. 45 × 35 cm, broadly obovate to broadly spathulate, glabrous, coriaceous, not glossy, apex caudate, base attenuate; midrib angular, lenticellate, prominent; margins glabrous, entire; secondary veins 18 or 19 pairs per side, eucamptodromous, abaxially prominent; domatia absent; stipules ca. 35 mm long, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads ca. 6 cm wide; inflorescence axes 16–21 cm long, flattened, puberulous; bracts calyptra-like, deciduous; peduncles not elongated. Flowers 5-merous; calyx tubes ca. 3 mm long, with prominulous ribs, inside lanate, outside glabrous except on upper parts of ribs, lobes ca. 2 mm long, oblong to truncate, pubescent; corolla tubes ca. 14 × 1.5 mm, ribbed, glabrous, lobes ca. 3 × 1 mm, oblong, inside glabrous, outside puberulous in upper third, margins ciliate; anthers ca. 2 mm long; filaments 0.25–0.5 mm long, flattened; styles 17–18 × ca. 0.25 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 8 per locule, pendulous, imbricate; placentae strongly flattened, elongated. Infructescences not seen.

Habitat and distribution. Habitat unknown; Madagascar.

Phenology. Unknown.

Discussion. *Breonia madagascariensis* is known only from the six authentic herbarium specimens collected by Commerson, Chapelier, and Bréon during the early botanical explorations they undertook separately in 1770–1771, 1794–1808, and 5 September–5 December 1818, respectively (Dorr, 1997). No collecting localities were mentioned on their labels. This species has not been collected since 1818.

Chapelier is known to have resided on the East Coast at Foulpointe for a dozen years, and he established an experimental garden in a place known locally as Isatrano (Tamatave or Toamasina). Also, he made botanical collections around Ivoloina, Foulpointe, and on the island of St. Marie (all within Toamasina province). Hence, it is possible that *Breonia madagascariensis* was collected from the above-mentioned areas of the east coast of Madagascar. Most of the eastern coast of the country has been deforested for agricultural purposes and replaced by secondary vegetation characterized by the dominance of *Ravenala madagascariensis* Sonn. (Strelitziaceae). However, *B. madagascariensis* may still be extant inside protected forests (Betampona Reserve, Zahamena Reserve, Analamazaotra Reserve) in this area, so efforts to rediscover *B. madagascariensis* should focus on these three protected areas and their surroundings.

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Figure 11. *Breonia louryi.*—A. Fertile branch with young infructescence. —B. Mature infructescence. —C. Seed, showing flattened lateral profile (left); dorsal view (right). —D. Median dissection through fruit, showing calyx tube and bicarpellate ovary with 7 to 9 pendulous ovules per locule (left); entire fruit (right). —E. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing glabrous corolla and pubescent calyx tubes and bicarpellate ovary with ovules (left); entire flower, showing only part of corolla tube (right). *Lewis et al. 755* (MO).

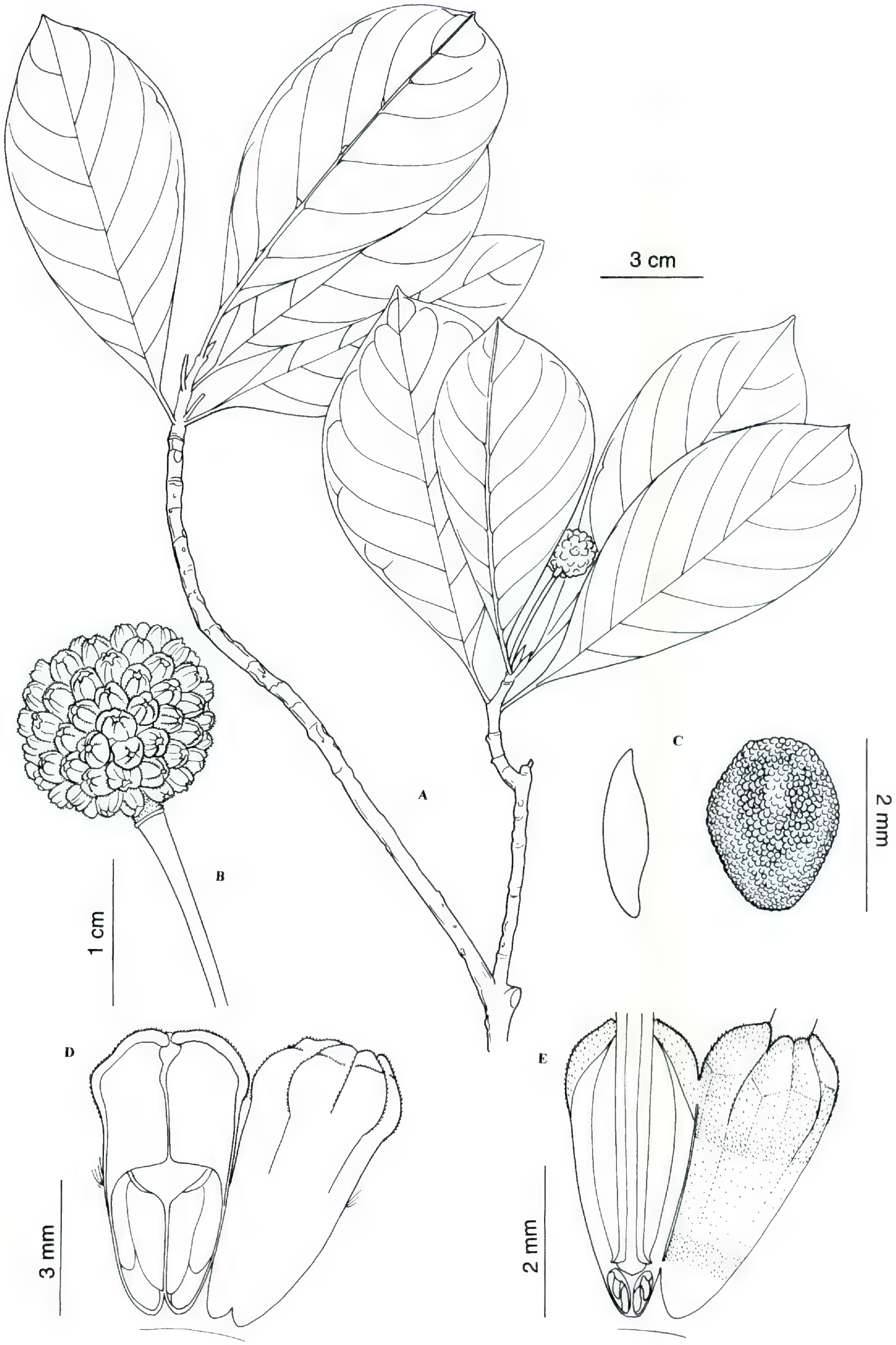
3 cm
A
B
1 cm
C
2 mm
D
3 mm
E
2 mm

Table 3. Distinctive vegetative morphological features separating *Breonia macrocarpa* and *B. madagascariensis*.

Characters	*Breonia macrocarpa*	*B. madagascariensis*
Petioles	well developed	subsessile
Leaf blade size	19–38 × 15–25 cm	45 × 35 cm
Abaxial indumentum on leaf blades	densely pubescent	glabrous
Midrib shape	rounded	angular
Domatia	present	absent
Peduncle length	8.5–12.5 cm	16–21 cm

The lectotype *Chapelier s.n.* selected by Ridsdale (1975) was from the six known collections.

Additional specimens examined. "Madagascar, Herbier E. Drake, *P-0013910* (P)"; "Madagascar, herbarium Richard, *P-00132909* (P)," *Bréon s.n.* (P), *Commerson s.n.* (P not seen).

12. Breonia membranacea Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: "Madagascar." [Without exact locality], *Perottet s.n.* (lectotype, designated by Ridsdale (1975: 545), P!).

Trees, 12–18 m tall. Bark rugose. Leafy stems terete, glabrous. Terminal vegetative buds conical, 10–20 × ca. 1.5 mm, puberulent at the base. Leaves persistent; petioles 3–6 mm long, adaxially canaliculate, puberulous when young, glabrescent; blades 8.5–12.2 × 4.5–5.4 cm, oblong, glabrous, membranaceous, adaxially glossy, apex broadly cuspidate to acute, base rounded; margins glabrous, entire; secondary veins ca. 8 pairs per side, eucamptodromous, adaxially prominulous; domatia hairy in the axils of the secondary veins; stipules 12–21 mm long, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads ca. 2.2 cm wide; inflorescence axes 4.5–5.5 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles ca. 3 mm long, glabrous. Flowers 5-merous; calyx tubes 1–1.2 mm long, inside lanate, outside glabrous, lobes 0.5–0.7 mm long, oblong, velutinous; corolla tubes ca. 5 × 0.5–0.7 mm, inside puberulous, outside glabrous, lobes ca. 2 mm long, obtuse to truncate, puberulous, margins ciliate; anthers ca. 1 mm long; filaments ca. 2 mm long, flattened, glabrous; styles 7–8 × ca. 0.5 mm, glabrous; stigmas capitate; ovary 2-carpellate; carpels syncarpous; ovules 3 per locule, flattened, pendulous, imbricate; placentae small, elongated. Infructescences 1.5–1.8 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, fibrous; disks accrescent, heart-shaped; seeds 1 to 3 per locule, flattened, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen lowland rainforests, littoral forests; Districts of Moramanga and Fénérive Est (Fig. 12).

Common names. Molompangady, Valotra.

Phenology. Flowering January to February; fruiting March to April.

Discussion. This species is distinct in its leaves with relatively short petioles. The lectotypification made by Ridsdale is questionable because the lectotype, *Perottet s.n.*, does not match with Haviland's (1897) remarks concerning the terminal vegetative buds of *B. membranacea*: "I have seen none [specimens] with the apex uninjured." *Perrottet s.n.* has an intact and uninjured apex and was annotated by Haviland as *Breonia membranacea*. Haviland clearly stated that the type specimen of *B. membranacea* was in the Paris herbarium. Haviland mentioned that the description of *Breonia mauritiana* was based on a single specimen; he did not mention that this was also the case for *B. membranacea*. Hence, he could possibly have seen more than one specimen of *B. membranacea*, although he did not cite any other specimens in the original description.

Haviland is known to have visited the herbaria at the British Museum (BM), Leiden (L), and Paris (P) (Haviland, 1897). However, from Kew (K), L, and P, I received only the specimen of *Perrottet s.n.* from P. It is possible that the "injured" specimens seen by Haviland are at BM. Ridsdale visited all three herbaria while preparing his revision of African and Madagascar Naucleeae (Ridsdale, 1975); he did not cite any syntype for *B. membranacea*. This implies that he saw only the specimen of *Perrottet s.n.* at Paris. Before one can attempt to resolve the nomenclatural problem of *B. membranacea*, one must visit BM, L, and P and look for possible specimens of *B. membranacea* annotated by Haviland.

Additional specimens examined. MADAGASCAR. **Toamasina:** District Fénérive-Est, Ampasina, Tampolo, *13094 SF* (TEF), *16496 SF* (TEF), *16621 SF* (P); District Moramanga, Forêt d'Analamazaotra, *Louvel 186* (P).

13. Breonia perrieri Homolle, Bull. Soc. Bot. Fr. 84: 461. 1937 [publ. 1938]. TYPE: Madagascar. [Toliara province]: Morondava, Forêt de Marofandilia, *Perrier de la Bâthie 3513* (lectotype, designated by Ridsdale (1975: 546), P!).

Medium-sized trees, ca. 8 to 15 m tall. Bark with longitudinal fissures. Leafy stems flattened, lenticellate, glabrous. Terminal vegetative buds conical, 9–11 × 3–4 mm, glabrous. Leaves deciduous; petioles 33–60 × 1.5–1.8 mm, terete, glabrous or pubescent toward the apex, lenticellate; blades 9–15 × 6–13

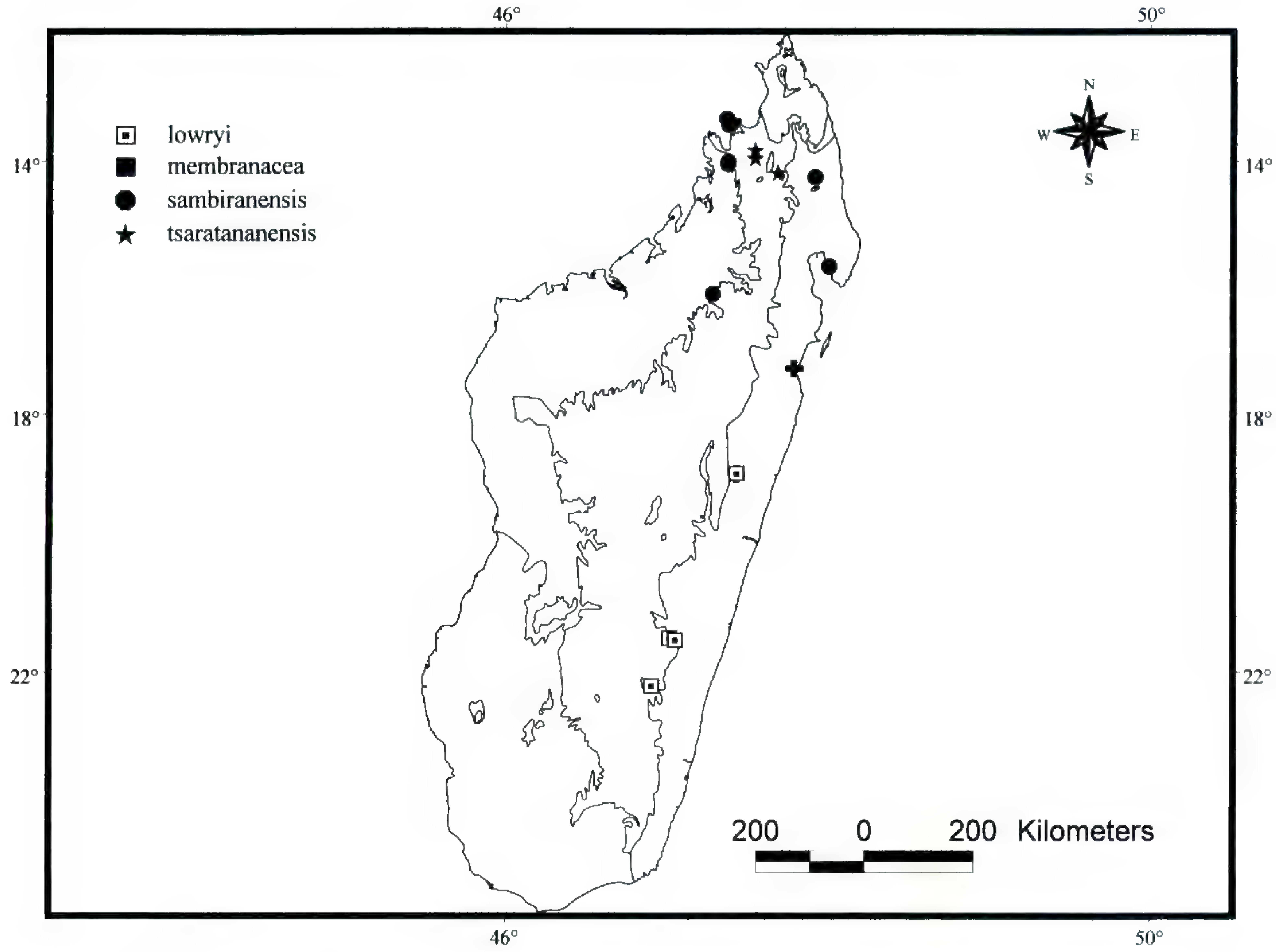

Figure 12. Distribution of *Breonia lowryi*, *B. membranacea*, *B. sambiranensis*, and *B. tsaratananensis*.

cm, broadly obovate to orbicular, pubescent or glabrous, coriaceous or rarely membranaceous, apex cuspidate to rounded, base cordate; margins glabrous, entire; secondary veins ca. 9 pairs per side, the first 3 diverging from the base of the midrib, prominulous; domatia absent; stipules 8–14 × 3–4.2 mm, cymbiform, abaxially carinate, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2.5–2.9 cm wide; inflorescence axes 2.4–3.5 cm long, terete, pubescent or glabrous; bracts calyptra-like, deciduous; peduncles 2–3 mm long. Flowers 5-merous; calyx tubes ca. 2.5 mm long, green, inside below the middle glabrous, velutinous from the middle toward the base of lobes, outside glabrous, lobes 1–1.2 mm long, oblong, puberulous; corolla tubes 4–5 × ca. 1 mm, yellow-tinged, glabrous, lobes ca. 1.5 mm long, oblong, glabrous; anthers 1–1.1 mm long; filaments ca. 1 mm long, flattened, glabrous; styles ca. 10 × 0.2 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 3 per locule, strongly flattened, pendulous, imbricate; placentae small, elongated. Infructescences 1.8–2.2 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, heart-shaped; seeds 1 to 2 per locule, with rudimentary wings at the base, strongly flattened, ellipsoid, white-tinged; seed-coat reticulate.

Phenology. Flowering November to January; fruiting January to March.

Habitat and distribution. Western and northwestern deciduous dry forests; from Districts of Antsiranana II and Ambato-Boeni, Befandriana-Nord, Soalala, Antsalova, Belo Tsiribihina, Maintirano, Marovoay, Ambilobe, and Vohémar (Fig. 5).

Common name. Valotra.

Phenology. Flowering November–December; fruiting January–February.

Discussion. The following were among the four specimens cited by Homolle in the protologue of *Breonia perrieri: Perrier de la Bâthie 825* (P not seen), *Perrier de la Bâthie 17852* (P not seen), and *Greve s.n.* (P not seen).

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Ankarana, Ambilomangodro, Forêt de Bezono, *29653 SF* (TEF); Mahamasina, Réserve Spéciale d'Ankarana, *Malcomber et al. 1833* (K, MO, P, TAN), *Razafimandimbison SG 273* (MO, P, TAN); Forêt d'Ambre, *6181 SF* (TEF), *6616 SF* (TEF); Plateau d'Ankarana à l'ouest d'Ambondromifehy, *3026 SF* (K, TEF); District Vohémar, Forêt d'Analafiana au nord de la base

Manambery, *27503 SF* (TEF); 14 km E of Vohémar, near Analafiana, *15673 SF* (TEF); Ankara, *6696 SF* (TEF). **Mahajanga:** District Ambato-Boeni, Ankirihitra, Forêt d'Anatialabe, *19379 SF* (TEF); District Befandriana-Nord, Ambahivahy, Forêt d'Andembikely, *19061 SF* (TEF); Forêt de Marohogo à l'ouest de Mahajanga, *18450 SF* (TEF); District Antsalova, à 3 km à l'Est de Bevitika, *Labat & Conté 2674* (K, MO, P, TAN), *Labat et al. 2261* (K, MO, P, TAN); Plateau de Bemaraha, aux environs de Tsiandro, *6754 SF* (TEF), *Jongkind et al. 3412* (K, MO, P, TAN), *Villiers et al. 4846* (MO, P, TAN); District Soalala, Commune Andranomavo, *3882 SF* (TAN), Andranomavo, *17565 SF* (TEF). **Toliara:** District Belo Tsiribihina, Tsimafana, Ankirijifotsy, *7987 SF* (TEF), *Noyes et al. 1028* (K, MO, P, TAN); District Morondava, Tsimembo-limite concession de M. Barthe, *8245 SF* (TEF); Ankilatsy, *4677 SF* (TEF).

14. Breonia richardsonii Razafim., sp. nov. TYPE: Madagascar. [Toamasina province]: Maroantsetra, Jardin botanique de Farankaraina, 16 June 1965 (fl), *14359 SF* (holotype, TEF). Figure 13.

Haec species a congeneris inflorescentiae bracteis tubulosis adpressis in 1 triangulares tres quatuorve desinentibus atque ovariis contiguis post anthesin distinguitur.

Trees, 15–30 m tall. Bark fissured longitudinally. Leafy stems terete, glabrous. Terminal vegetative buds conical, 3–4 × 1–1.5 mm, glabrous. Leaves persistent; petioles 7–10 × ca. 1 mm, terete, glabrous; blades 5–7.7 × 2.5–3.7 cm, oblanceolate to ovate, glabrous, membranaceous, apex cuspidate to acute, base acute; margins glabrous, entire; secondary veins 5 to 7 pairs per side, eucamptodromous, inconspicuous; domatia cryptic-type in the secondary veins, glabrous, adaxially prominent; stipules ca. 5 × 1–1.5 mm, cymbiform, not carinate, free at the base, deciduous. Inflorescence solitary, heads ca. 2 cm wide; inflorescence axes 2.5–3 cm long, terete, glabrous; peduncles ca. 5 mm long; bracts tubular with 3–4 broadly triangular lobes, not enclosing the young inflorescence, persistent. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 1 mm long, inside glabrous, except at the base velutinous, outside at the base velutinous, in the mid-parts glabrous, toward the lobes puberulous, lobes broadly triangular, puberulous; corolla tubes ca. 4 × 0.3–0.5 mm, glabrous, lobes ca. 1.5 mm long, oblong, glabrous; anthers 2–2.5 mm long; filaments ca. 0.1 mm long, flattened; styles ca. 7 × 0.5 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate, adjacent ovaries fused only at the base; carpels syncarpous; ovules 5 per locule, pendulous, imbricate; placentae large, elongated, occupying the upper third of the locule. Infructescences 1–1.5 cm diam., with well-developed calyx remnants, adjacent ovaries fused up to the mid-point; individual fruits with endocarp soft, fibrous; disks accrescent, obconical; seeds 5 per locule, strongly flattened, ellipsoid, angular, red; seedcoat reticulate.

Habitat and distribution. Lowland rainforests; District of Maroantsetra (Fig. 10).

Common names. Valotrafotsy.

Phenology. Flowering April; fruiting November.

Discussion. This species is very different from other species of *Breonia* because of its tubular, appressed inflorescence bracts with 3 to 4 broadly triangular lobes and post-anthesis fusion of adjacent ovaries. The specific epithet honors Mick Richardson, who was my Ph.D. advisor as well as the Manager of the Graduate Program at the Missouri Botanical Garden. This species is extremely rare and has not been collected since 1965.

Paratype. MADAGASCAR. **Toamasina:** District Maroantsetra, Jardin botanique de Farankaraina, *18311 SF* (TEF).

15. Breonia sambiranensis Razafim., sp. nov. TYPE: Madagascar. [Antsiranana province]: Nosy be, Réserve Naturelle Integrale de Lokobe, 13°24′S, 48°20′E, 350 m, 7 July 1995 (fl), *Antilahimena 237* (holotype, TAN; isotype, MO). Figures 3C, 4D, and 14.

Haec species a congeneris calycis tubo brevi prominule costato et lobulis brevibus in centro non profunde foveolatis, ad margines protuberationes breves stylum versus directas gerentibus distinguitur.

Trees, rarely shrubs, (6–)10–20 m tall. Bark smooth, glabrous. Leafy stems quadrangular, glabrous, lenticellate. Terminal vegetative buds conical, ca. 5 × 2–3 mm, glabrous. Leaves persistent; petioles 15–30 mm long, adaxially canaliculate, glabrous; blades (8.5–)12–17.5 × 4.7–9.5 cm, broadly ovate to broadly obovate, or broadly ovate to narrowly ovate, glabrous, coriaceous, glossy, apex mucronulate to acute or mucronulate to obtuse, base cuneate, lower surfaces yellow-red-tinged when dry; margins entire, glabrous; secondary veins 5 to 9 per side, eucamptodromous, dark red when dry, abaxially prominulous; domatia absent; stipules 6–7 × 4–5 mm, cymbiform, not carinate, glabrous, free at the base, deciduous. Inflorescence solitary, heads 3–3.7 cm wide; inflorescence axes 2.5–3 cm long, flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1.5–2.2 mm long, glabrous. Flowers 5-merous; calyx tubes 1–1.2 mm long, infundibular, prominulously ribbed, glabrous; lobes 0.2–0.3 mm long, truncate, bearing a shallow depression in the center, a short protuberance on the edge toward the style (Fig. 14D), tomentose; corolla tubes 7–8 × 0.8–0.9 mm, inside puberulous, outside glabrous, lobes ca. 3 mm long, oblong,

recurved, with protuberance abaxially (Fig. 14E), glabrous, with a few scattered hairs at the apex, ciliate; anthers ca. 1.2 mm long; filaments 0.1–0.2 mm long; styles ca. 13 × 0.1 mm; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 4 to 5 per locule, flattened, imbricate; placentae elongated, strongly flattened. Infructescences 1.2–1.6 cm diam., with accrescent calyx remnants; individual fruits with endocarps soft, fibrous; disks accrescent, napiform; seeds 4 to 5 per locule, concavo-convex, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. This species occurs in low- and mid-altitude evergreen rainforests; Districts of Nosy Be, Ambanja, and Maroantsetra (Fig. 12).

Common name. Valotra.

Phenology. Flowering March to July; fruiting October to November.

Discussion. This species is distinct in its short calyx tubes prominulously ribbed, short calyx lobes with shallow depressions in the center, and short protuberances on the edge toward the style (Fig. 14D). The specific epithet refers to the Sambirano regions.

Paratypes. MADAGASCAR. **Antananarivo:** District Ankazobe, Forêt d'Ambohitantely, *8413 SF* (TEF). **Antsiranana:** District Ambanja, Manongarivo Special Reserve, Massif de Bekolosy, *11430 SF* (TEF); District Nosy be, Lokobe, *9220 SF* (TEF), *11407 SF* (TEF), *24753 SF* (TEF), *5524 RN* (TEF), *Birkinshaw 59* (K, MO); Bemarivo, Androranga, ravin de Betsomanga, *841 SF* (K, MO, TEF). **Toamasina:** District Maroantsetra, Masoala Peninsula, S of the village of Ambanizana, *Behasy & Vasey 203* (MO), *Rabe 115* (MO).

16. Breonia sphaerantha (Baill.) Homolle ex Ridsdale, Blumea 22: 546. 1975. *Franchetia sphaerantha* Baill., Bull. Soc. Linn. Paris 60: 477. 1885. TYPE: Madagascar. [Without exact locality], *Hildebrandt 3309* (holotype, P!; isotypes, K!, L!).

Elattospermum longipetiolatum Soler., Bull. Herb. Boissier 1: 277. 1893. TYPE: Madagascar. [Without exact locality], *Hildebrandt 3309* (holotype, L!; isotypes, K!, P!). Figure 2B.

Breonia parviflora Havil., J. Linn. Soc. Bot. 33: 37. 1897. TYPE: "Madagascar." [Without exact locality], *Hildebrandt 3309* (holotype, K!; isotypes, L!, P!).

Shrubs to large trees, 7–18 m tall. Bark white-tinged, rugose. Leafy stems terete, puberulous to pubescent, lenticellate. Terminal vegetative buds, conical, 2–3 × 1.2–1.5 mm, puberulous. Leaves persistent; petioles 15–20 × 0.9–1 mm, terete, puberulous; blades 5.2–6.7 × 2.5–3.9 cm, elliptic to oblanceolate (oblong to oblanceolate), adaxially glabrous, abaxially puberulous, membranaceous, glossy, apex acuminate, base rounded to truncate; margins glabrous, entire; secondary veins ca. 7 pairs per side, eucamptodromous, barely evident on upper surfaces, red-tinged when dry; domatia pocket-type in the axils of secondary veins, glabrous; stipules ca. 5 × 2 mm, cymbiform, not carinate, puberulous, free at the base, deciduous. Inflorescence solitary, heads 1–1.2 cm wide; inflorescence axes 2.4–3.8 cm long, usually bent and twisted when dry, terete, pubescent to velutinous; bracts calyptra-like, deciduous; peduncles ca. 1 mm long. Flowers mostly 4-merous or rarely 5-merous; calyx tubes ca. 1 mm long, green-yellow-tinged, inside velutinous, outside pubescent, lobes ca. 0.5 mm long, triangular, pubescent; corolla tubes 4.2–4.3 × ca. 0.2 mm, yellow-tinged, glabrous, lobes ca. 1.2 mm long, elliptic, lower parts glabrous, toward the apex puberulous, ciliate; anthers ca. 1 mm long; filaments ca. 0.2 mm long, terete, glabrous; styles 6–7 × ca. 0.8 mm, glabrous; stigmas globose to clavate; ovary 2-carpellate; carpels coherent; ovule 1 per locule, pendulous; placentae small, ovate. Infructescences 4–10 mm diam., densely pubescent, with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, obconical; seeds 1 per locule, with one side convex, the other flattened, ellipsoid, red; seed-coat lineate.

Habitat and distribution. Lowland evergreen rainforests; Districts of Antsiranana II, Nosy Be, Ambanja, and Befandriana-Nord (Fig. 10).

Phenology. Flowering January–July; fruiting March–December.

Discussion. Baillon (1885), Solereder (1893), and Haviland (1897) all used different sheets of the same collection, *Hildebrandt 3309*, as the basis for *Franchetia sphaerantha*, *Elattospermum longipetiolatum*, and *Breonia parvifolia*, respectively. Neither Solereder nor Haviland knew about *Franchetia sphaerantha*, and Haviland did not cite *Elattospermum longipetiolatum* either.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Antsiranana II, Canton Anamakia, Ankotikona, *15273 SF* (TEF); bords de rivière Kongony, Ambaliha, *2950 SF* (TAN, TEF); District Nosy be, Lokobe Reserve, *Antilahimena 82* (K, MO); Lokobe, *7822 RN* (TAN), *9229 RN* (TAN), *9453 RN* (TEF), *11417 SF* (TEF), *24764 SF* (TEF); District Ambanja, *Randrianaivo 255* (MO); Canton Marovato, Beangona, *Rakoto 9* (TAN). **Mahajanga:** District Befandriana-Nord, Commune Tsarahonenana, Forêt domaniale d'Antetezana, *15947 SF* (TEF); [unknown locality], *6257 RN* (TEF).

17. Breonia stipulata Havil., J. Linn. Soc. Bot. 33: 35. 1897. TYPE: "Madagascar, Northwest" [without exact locality], 1841 (fr), *Pervillé s.n.* (holotype, P!).

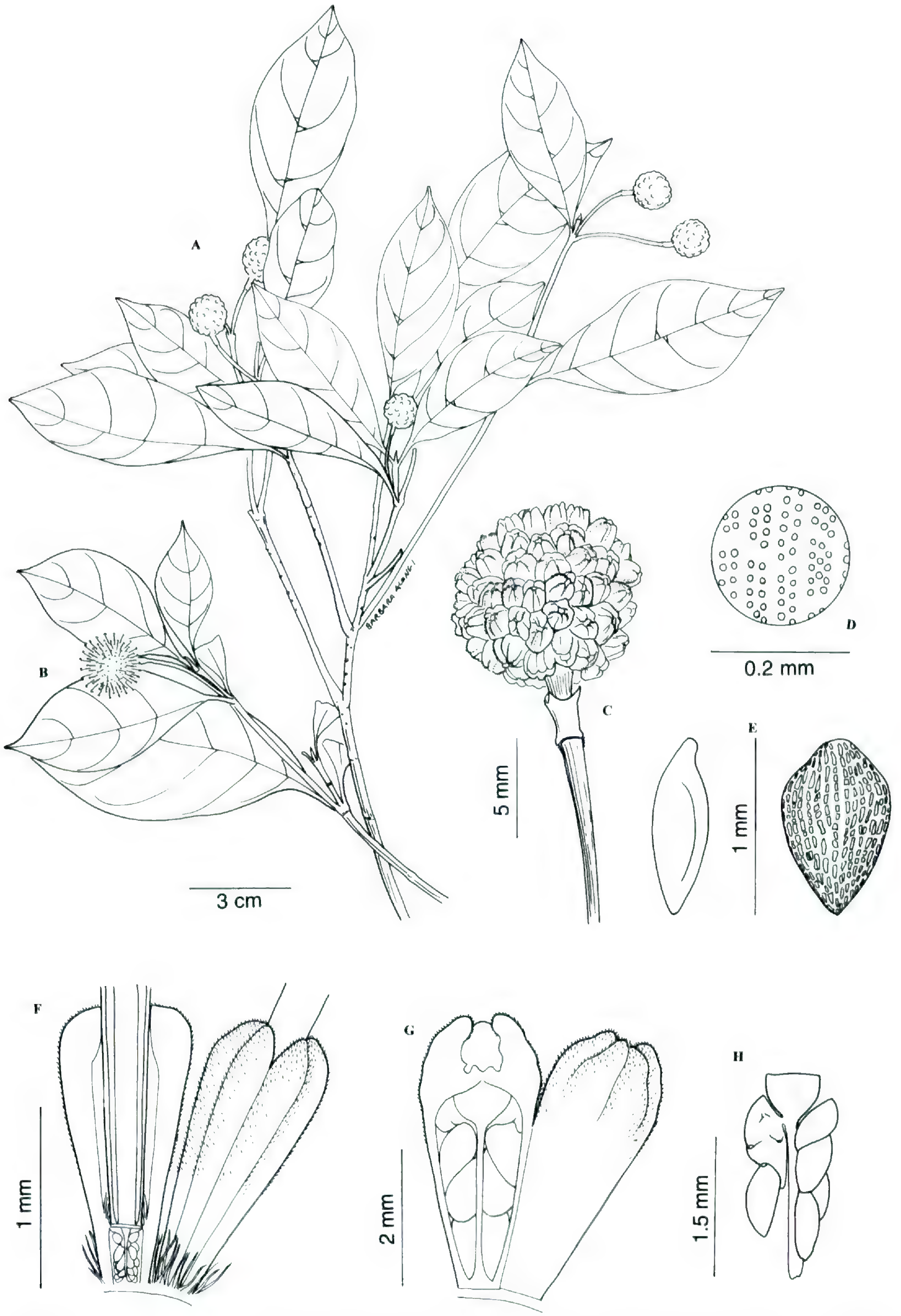

Figure 13. *Breonia richardsonii.*—A. Fertile branch with mature infructescences. —B. Fertile branch with inflorescence. —C. Mature infructescence, bearing a tubular bract. —D. Seed surface. —E. Seed, lateral view (left); dorsal

Trees or shrubs, 15–25 m tall. Bark rugose. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 19–22 × 2–3 mm, glabrous. Leaves deciduous; petioles 12–22 × 1.5–2 mm, adaxially canaliculate, glabrous; blades 10–18.5 (–24.5) × 4.5–6(–8) cm, elliptic to lanceolate, glabrous, coriaceous, not glossy, both apex and base acute; margins glabrous, entire; secondary veins (9–)11 or 12 pairs per side, eucamptodromous, abaxially prominulous; domatia absent (hairy or crypt-type domatia in the axils of secondary veins); stipules 15–18 × 2.2–2.5(–3) mm, cymbiform, narrowly carinate abaxially, glabrous, free at the base, deciduous. Inflorescences solitary, heads 2.2–2.5 cm wide; inflorescence axes 4–6 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1 mm long. Flowers 5-merous or rarely 4-merous; calyx tubes ca. 2 mm long, inside lanate, outside glabrous, toward the lobes puberulous, lobes ca. 1 mm long, oblong, tomentose; corolla tubes ca. 5 × 0.9–1 mm, glabrous, lobes 1.5–2 mm long, oblong, glabrous; anthers ca. 1.5 mm long; filaments 0.2–0.3 mm long; styles ca. 10 × 1 mm, glabrous; stigmas clavate to slightly cylindrical; ovary 2-carpellate; carpels syncarpous; ovules 1 to 2 per locule, pendulous, imbricate; placentae ovate, small. Infructescences 1.5–1.7 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, heart-shaped; seeds 1 per locule, pendulous, concavo-convex, ellipsoid, both ends acute, red; seed-coat reticulate.

Habitat and distribution. Deciduous dry forests; Districts of Maintirano, Sambava, Andapa, Antsiranana II, and Antsalova (Fig. 10).

Common names. Valitsy and Vaomolompangady.

Phenology. Flowering October to December; fruiting December to February.

Additional specimens examined. MADAGASCAR. **Antsiranana:** District Andapa, Mandena, Forêt de Marojejy, *Rakotozafy & Raharilala 2189* (TAN); lisière de forêt, *Rakotozafy & Raharilala 2271* (TAN); trail to the summit of Marojejy Est, NW of Mandena, *Miller 3609* (K, MO, P, TAN); District Antsiranana II, Anivorano-Nord, Ambararatamisakana, *15057 SF* (TEF). **Mahajanga:** District Antsalova, 1 km à l'Est de Bevitika, *Labat et al. 2263* (K, MO, P); Botomena, *11089 RN* (TEF); Tsiandro, Forêt d'Antsingy aux environs de la clairière de piste d'Ambodiriana, *6791 SF* (TEF), *12023 SF* (TEF), *18029 SF* (TEF); Forêt de Valoala, [*collector unknown*], *2200* (TAN).

18. Breonia taolagnaroensis Razafim., sp. nov. TYPE: Madagascar. [Without exact locality], *Commerson s.n.* (holotype, P!). Figure 2F.

Haec species a congeneris disco nectarifero pentagono accrescente permagno distinguitur; ex sylvis littoralibus prope Taolagnaro tantum cognita.

Shrubs, 4–6 m tall. Bark rugose with annular fissures. Leafy stems quadrangular, glabrous. Terminal vegetative buds conical, 5–6 × ca. 3 mm, glabrous. Leaves persistent; petioles 13–20 × ca. 2.5 mm, adaxially canaliculate, glabrous; blades 9–11(–16) × 3.5–6.5 cm, ovate to oblong, glabrous, coriaceous, glossy, apex rounded to broadly cuspidate, base cuneate; margins glabrous, entire; secondary veins (7–)9 to 10 pairs per side, eucamptodromous; domatia absent; stipules 6–10 mm long, cymbiform, not carinate, free at the base, glabrous, deciduous. Inflorescence not seen; inflorescence axes (4–)6–8.5 cm long, strongly flattened; bracts not seen; peduncles absent. Flowers not seen. Infructescences 1.5–2 cm diam., with well-developed calyx remnants; individual fruits with endocarp hard, glossy; disks accrescent, pentagonal; seed 1 per locule, concavo-convex, with rudimentary wings at both ends, red; seed-coat reticulate.

Habitat and distribution. Littoral forests and evergreen rainforests; Districts of Fort-Dauphin and Farafangana (Fig. 10).

Common names. Valotr'angady, Molompangady, and Marotsaka.

Phenology. Flowering unknown; fruiting October to December.

Discussion. Bosser (1984) argued that the type specimen of *Cephalidium citrifolium* (Poir.) A. Rich. is the *Commerson* collection on which I base *Breonia taolagnaroensis.* I disagree with Bosser because *Commerson s.n.* now in P has fruits only, but Richard used a specimen with both flower and fruit on which to base his *Cephalidium. Commerson s.n.* has a flower only and matches Poiret's original descriptions of his *Nauclea citrifolia.*

Breonia taolagnaroensis is distinguished from the other species of *Breonia* by its massive, accrescent pentagonal disks, and is known only from the littoral forests of the Taolagnaro (Fort-Dauphin) regions, thus the specific epithet. The type specimen of this

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view (right). —F. Median dissection through flower, showing bicarpellate ovary with numerous ovules (left); entire flower, showing part of corolla tube (right). —G. Dissection through a calyx remnant and a carpel of a separate fruit (left); entire individual fruit (right). —H. Naked carpel, showing an accrescent disk adnate to the septum and 5 ovules attached to the placentae. A–F from *14359 SF* (TEF) and G from *18311 SF* (TEF).

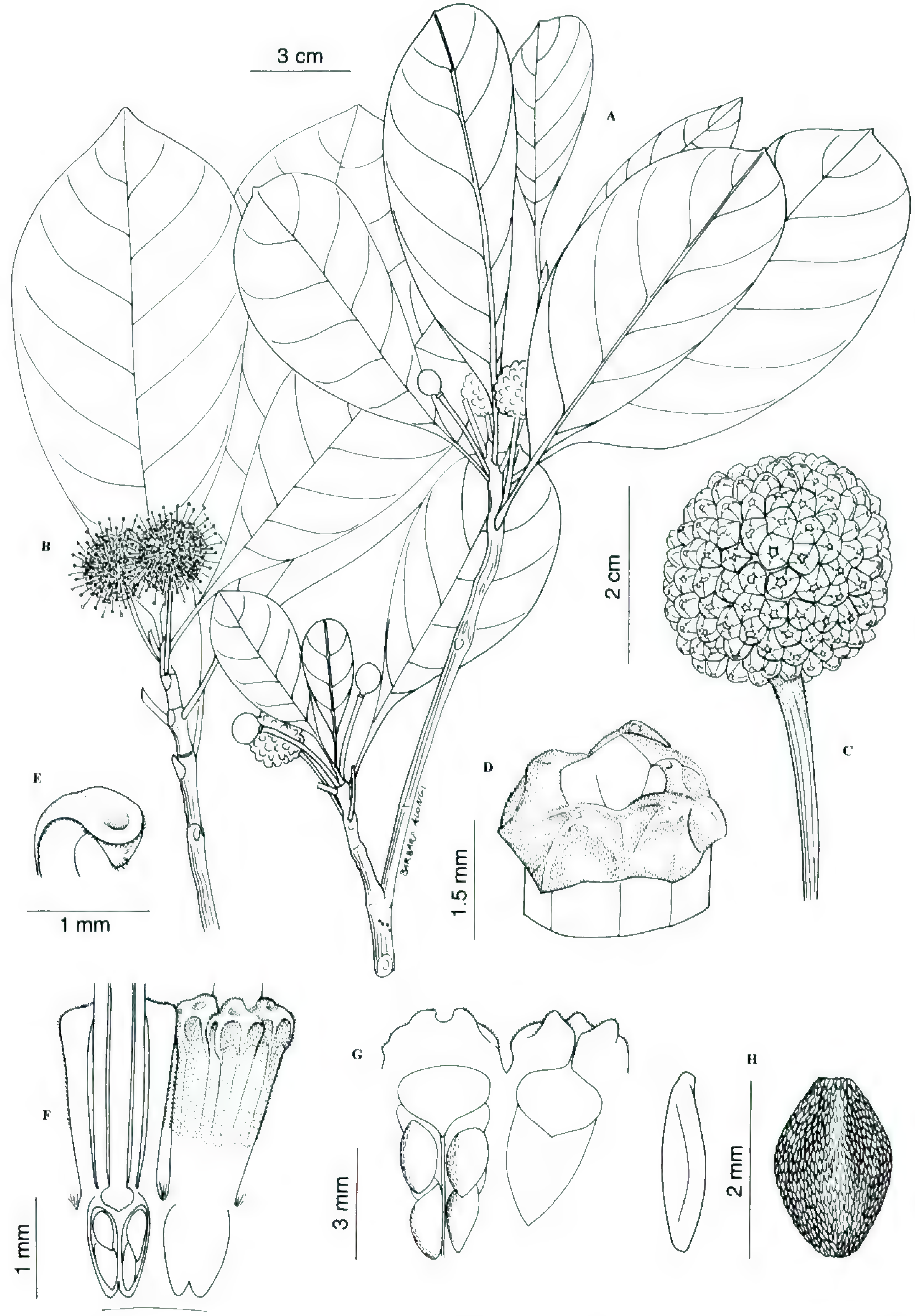

Figure 14. *Breonia sambiranensis*.—A. Fertile branch with infructescences. —B. Fertile branch with inflorescences. —C. Mature infructescence. —D. Calyx. —E. A corolla lobe bearing a protuberance. —F. Two adjacent flowers, showing two adjacent ovaries separated; median dissection through flower, showing a calyx and corolla tubes, and ovary (left);

species was identified by Capuron (1973b) as *Breonia chinensis* (Lam.) Capuron; however, it is distinguished from *B. chinensis* by having bark with annular fissures and by a single ovule per locule.

Paratypes. MADAGASCAR. **Fianarantsoa:** District Farafangana, Horombe, *4855 SF* (TEF); Forêt de Manombo, *23641 SF* (TEF). **Toliara:** District Fort-Dauphin, Forêt d'Analalava, *Dumetz 1367* (K, MO); Forêt d'Ilandy au Nord de Fort-Dauphin, *20558 SF* (TEF), *McPherson 14391* (K, MO, TEF); Manantenina, Beharena, *10925 SF* (TEF).

19. Breonia tayloriana Razafim., sp. nov. TYPE: Madagascar. Toamasina: Fénérive Est, Tampolo, 3 Jan. 1956 (fl), *15703 SF* (holotype, TEF). Figure 15.

Haec species a congeneris stipulis semipersistentibus amplis abaxialiter carinatis perfacile distinguitur.

Medium-sized trees, 9–10 m tall. Bark longitudinally fissured. Leafy stems quadrangular, lenticellate, glabrous. Terminal vegetative buds conical, 13–30 × 7–10 mm, glabrous. Leaves persistent, petioles 22–35 × 2–4.5 mm, adaxially canaliculate, glabrous; blades 18–32 × 10–15.5 cm, broadly obovate to broadly ovate, reddish, glabrous, coriaceous, glossy, apex obtuse to rounded, base cuneate; margins glabrous, entire; secondary veins 7 to 9 pairs per side, eucamptodromous, prominulous; without domatia; stipules 19–31 × 9–12.1 mm, cymbiform, abaxially carinate, glabrous, united at the base, semi-persistent. Inflorescences solitary (2 per axil), heads 3.2–3.5 cm wide; inflorescence axes 3.2–4.2 cm long, strongly flattened, glabrous; bracts calyptra-like, deciduous; peduncles 1–2 mm long. Flowers 5-merous; calyx tubes ca. 2 mm long, green, inside lanate, outside glabrous, lobes ca. 1.7 mm long, oblong to truncate, lanate; corolla tubes 8–9 × ca. 1 mm, light beige to cream, inside puberulous, outside glabrous, lobes ca. 1.8 mm long, oblong, at the lower parts glabrous, puberulous toward the apex; anthers ca. 1 mm long; filaments ca. 0.1 mm long, glabrous, terete; styles ca. 13 × 0.2 mm, glabrous; stigmas clavate; ovary 2-carpellate; carpels syncarpous; ovules 2 to 4 per locule, strongly flattened, pendulous, imbricate; placentae elongated. Infructescences 2–2.4 cm diam., with well-developed calyx remnants; individual fruits with endocarp soft, fibrous; disks accrescent, obconical; seeds 1 to 2 per locule strongly flattened, ellipsoid, red; seed-coat reticulate.

Habitat and distribution. Evergreen rainforests and littoral forests; Districts of Maroantsetra, Brickaville, and Fénérive Est (Fig. 10).

Common names. Molompangady mena (red lips of spade).

Phenology. Flowering December to February; fruiting February to April.

Discussion. The specific epithet honors Charlotte Taylor, a Rubiaceae specialist who has studied mostly the Neotropical Rubiaceae. Charlotte has taught me various aspects of taxonomy, including nomenclature, describing new species, writing a monograph, herbarium curation, and specimen annotation. The present revision was carried out under her supervision.

Paratypes. MADAGASCAR. **Toamasina:** District Fénérive-Est, Canton Ampasina, Itampolo, *Zavah Paul 321-R-107* (TEF); District Brickaville, Ambila Lemaitso, Ampanotoamaizina, *8317 SF* (TEF); District Maroantsetra, Masoala peninsula, coastal sand forest just N of Antalavia, *Schatz et al. 1912* (K, MO, P, TAN); Jardin botanique de Farankaraina, *5652 SF* (TEF), *63-R-199* (TEF); [Locality unknown], *32928 SF* (TEF).

20. Breonia tsaratananensis Razafim., sp. nov. TYPE: Madagascar. [Antsiranana province]: Massif de Tsaratanana, haut bassin de la Beandrarezina (Andranomena), affluent rive gauche de la Mahavavy, 2000–2300 m, 11 Nov. 1966 (fr), *27049 SF* (holotype, TEF). Figure 16.

Haec species a congeneris tubo calycino supra medium dilatato apicem basemque constricto facile distinguitur.

Trees, 15–30 m tall. Leafy stems quadrangular, glabrous. Bark rugose. Terminal vegetative buds conical, 8–9 × ca. 3 mm, glabrous. Leaves persistent, petioles 15–20 mm long, adaxially canaliculate, glabrous; blades 9.5–11.3 × 5.2–6.5 cm, elliptic to obovate, glabrous, coriaceous, brittle when dry, glossy, apex mucronulate, base attenuate; margins glabrous, revolute, entire; secondary veins ca. 7 pairs per side, orange to yellow-tinged, eucamptodromous, prominulous; cryptic-type domatia at the base of the secondary veins, evident, ovate, glabrous; stipules ca. 10 × 3 mm, cymbiform, not carinate, glabrous, deciduous. Inflorescences solitary, heads ca 1.7 cm wide; inflorescence axes 2.5–3.3 cm long, slightly flattened, woody, densely pubescent; bracts calyptra-like, deciduous; peduncles ca. 1–2 mm long, densely pubescent. Flowers 5-merous or rarely

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entire flower (right). —G. Two adjacent fruits, showing two adjacent carpels separated: median dissection of mature infructescence, showing accrescent disk and seeds. —H. Seed, dorsal view (left); lateral view (right). A–F from *Antilahimena 237* (MO) and G from *11407 SF* (TEF).

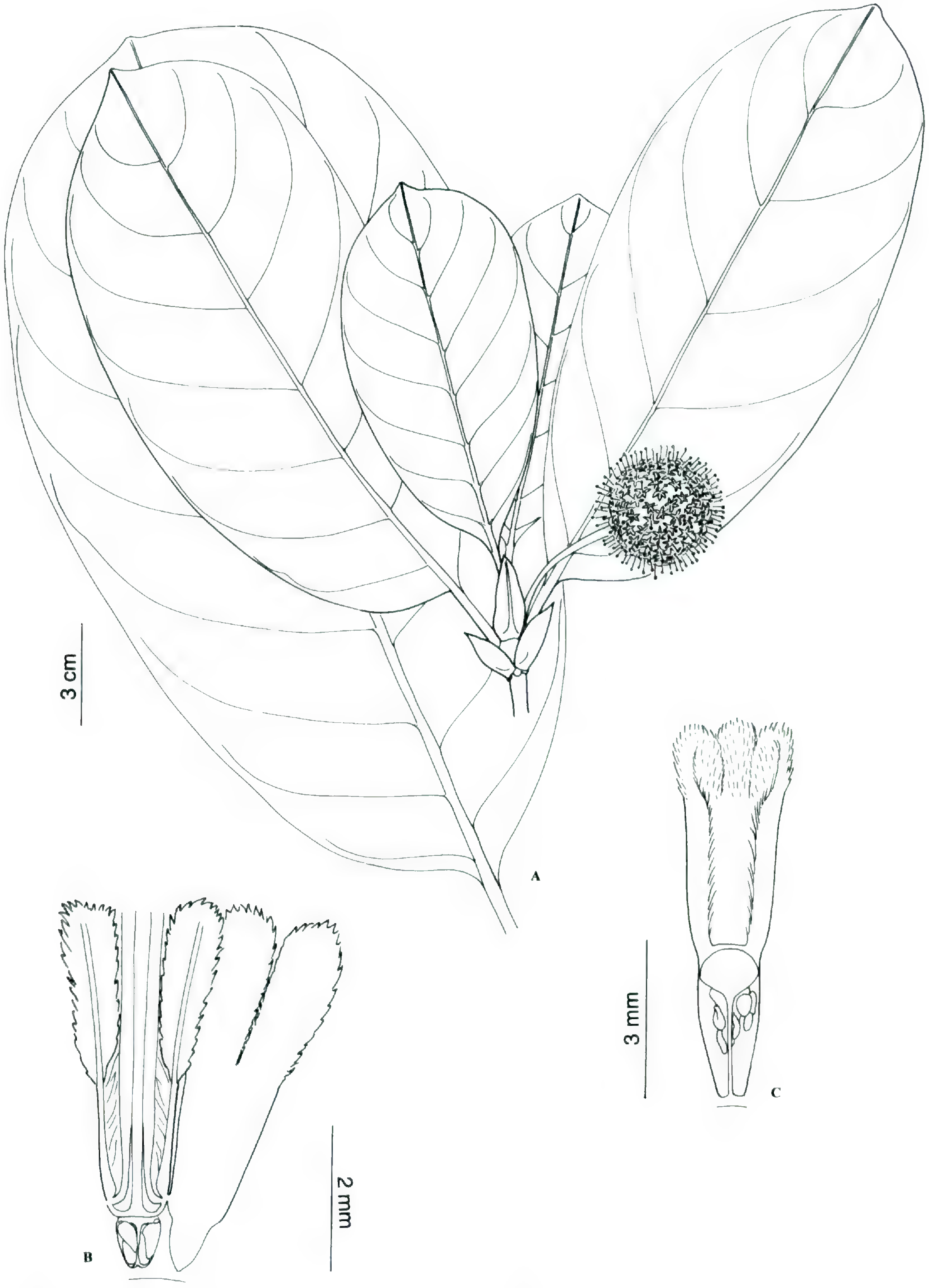

Figure 15. *Breonia tayloriana*.—A. Fertile branch with inflorescence and semi-persistent stipules. —B. Two adjacent flowers, showing two adjacent ovaries separated: median dissection through flower, showing lanate calyx and ovaries (left); entire flower (right). —C. Median dissection through a separate fruit, showing accrescent disk and ovaries with young seeds. A–C from *15703 SF* (TEF).

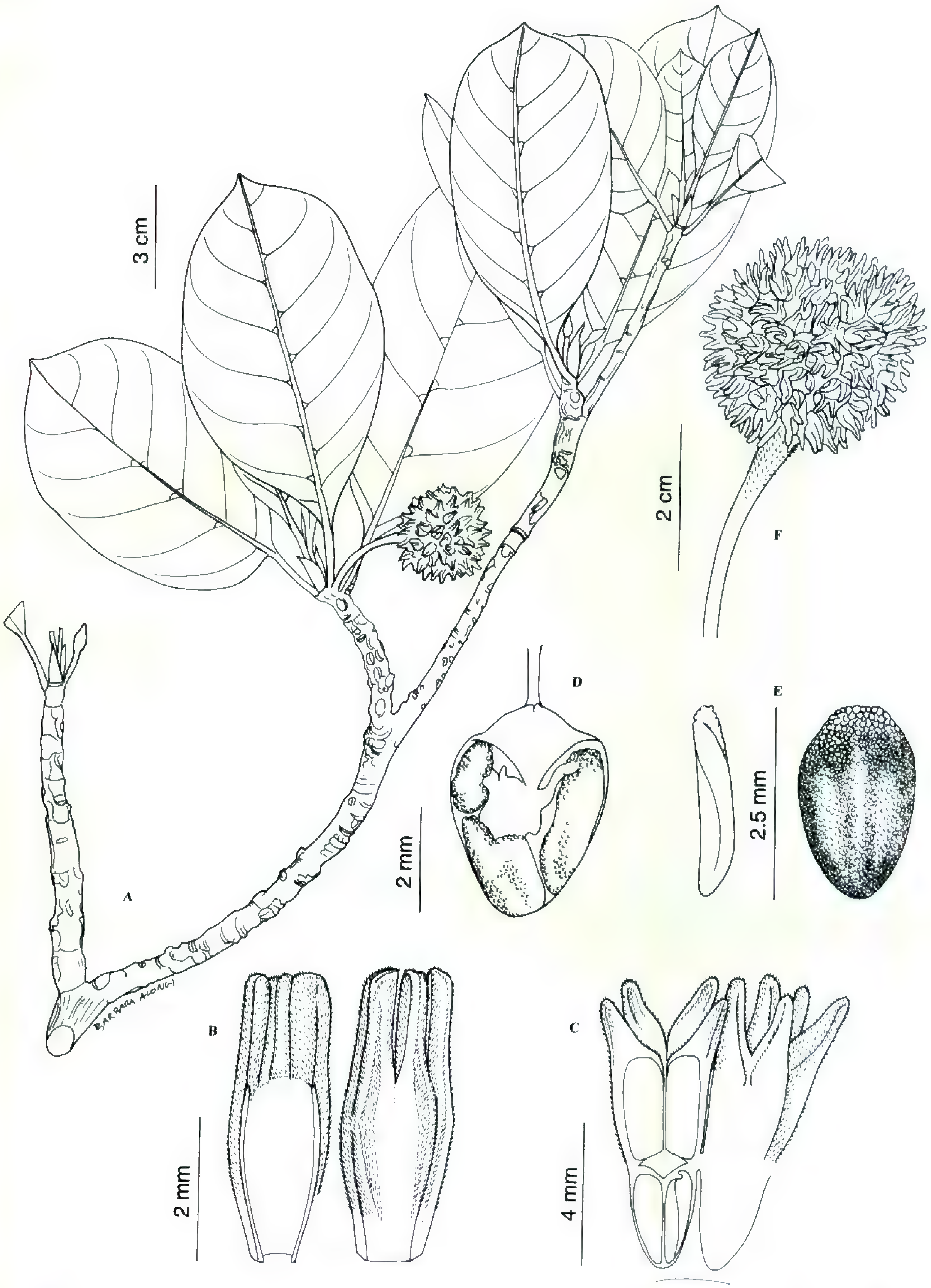

Figure 16. *Breonia tsaratananensis.*—A. Fertile branch with a young inflorescence and a mature infructescence. —B. Two adjacent flowers, showing two adjacent ovaries separated: median dissection of calyx with adaxial view (left); abaxial view (right). —C. Median dissection through fruit, showing accrescent disk and carpels with seeds (left); entire fruit (right). —D. Dissected unilocular ovary. —E. Mature seed: dorsal (left); lateral (right). —F. Mature infructescence. A, B from *973 SF* (TEF) and C–F from *27049 SF* (TEF).

4-merous; calyx tubes ca. 2.5 mm long, dilated above the middle, constricted at both ends, prominently ribbed, inside glabrous, outside puberulous, lobes truncate, ribbed, quadrangular, tomentose; corolla tubes 5–6 mm long, inside pubescent, outside puberulous; lobes ca. 2 mm long, recurved, puberulous; anthers not seen; style 7–8 mm long, glabrous; stigmas clavate; ovary 2-carpellate, rarely 1-carpellate; carpels syncarpous; ovules 3 to 5 per locule, pendulous, flattened, imbricate; placentae large, elongated. Infructescences 2–2.5 cm diam., with accrescent calyx remnants, persistent on the branches until the next flowering season; individual fruits with endocarp soft, fibrous; disks accrescent, triangular, seeds 3 to 4 per locule, concavo-convex, ellipsoid, dark red; seed-coat reticulate.

Habitat and distribution. Mid- and high-altitude humid forests; District Ambanja (including Tsaratanana Mountain) (Fig. 12).

Common name. Valotro.

Phenology. Flowering December to February; fruiting March to November.

Discussion. This species is known from five collections made from three individual trees; therefore, it is considered to be rare. Also, this is one of the two species of *Breonia* found only in high-altitude (above 1500 m) humid forests.

The specific epithet refers to the highest Malagasy mountain, Tsaratanana (2880 m), where the type species was collected.

Paratypes. MADAGASCAR. **Antsiranana:** District Ambanja, Massif de Tsaratanana, vallée de la Mahavavy, *Morat 2306* (MO, TAN). **Mahajanga:** Mangindrano, Ambohimirahavavy, *973 SF* (K, MO, TEF).

Dubious Species

Breonia longipetiolata Havil., J. Linn. Soc. Bot. 33: 36. 1897. TYPE: *Leprieur s.n.* (P!). This specimen, definitely belonging to *Breonia*, was reported to have been collected by Leprieur from French Guiana. However, the locality must be considered doubtful because *Breonia* is restricted to Madagascar and has never been reported from South America. Also, Leprieur never collected plants in Madagascar. The type and only specimen of *B. longipetiolata* does not match any of the species recognized here. This species is distinguished by its leaf blades with acute to rounded apices and long (ca. 9.6 cm) and strongly flattened peduncles.

Excluded Species

Breonia mayorii Setch. = *Sarcopygme mayorii* (Setch.) Setch. & Christoph. This species was originally placed in *Breonia* simply because of its multiple fruits. It has been transferred to the genus *Sarcopygme* of the tribe Morindeae based on the presence of raphides and bifid stigmas.

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Appendix 1.

List of species

1. *Breonia boivinii* Havil.
2. *Breonia capuronii* Razafim.
3. *Breonia chinensis* (Lam.) Capuron
4. *Breonia cuspidata* (Baker) Havil.
5. *Breonia decaryana* Homolle
6. *Breonia fragifera* Capuron ex Razafim.
7. *Breonia havilandiana* Homolle
8. *Breonia louvelii* Homolle
9. *Breonia lowryi* Razafim.
10. *Breonia macrocarpa* Homolle
11. *Breonia madagascariensis* A. Rich.
12. *Breonia membranacea* Havil.
13. *Breonia perrieri* Homolle
14. *Breonia richardsonii* Razafim.
15. *Breonia sambiranensis* Razafim.
16. *Breonia sphaerantha* (Baill.) Homolle ex Ridsdale
17. *Breonia stipulata* Havil.
18. *Breonia taolagnaroensis* Razafim.
19. *Breonia tayloriana* Razafim.
20. *Breonia tsaratananensis* Razafim.

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Examined specimens are listed alphabetically by collector, followed by collection numbers; the species is indicated by a number in parentheses corresponding to the number in the List of Species.

Andrianarisata et al. 259 (6); Antilahimena 19 (1), 44 (1), 82 (16), 237 (15); Antilahimena et al. 324 (6).

Baron 5563 (4), 6602 (4); Behasy & Vasey 203 (15); Bernard 187 (3), 327 (3); Bernardi 11899 (13); Birkinshaw 59(15), 67 (1); Boivin s.n. (1).

Chapelier s.n. (3), s.n. (11); Commerson s.n. (3), s.n. (3), (P-LA) (3), s.n. (18).

Decary 5199 (5), 5511 (3), 5513 (3), 5573 (3); Dumetz 1367 (18).

Gautier 3772 (2); Gautier et al. 3288 (6).

Hildebrandt 3309 (16); Humblot s.n. (3).

Jongkind et al. 3412 (13).

Labat et al. 2261 (13), 2263 (17), Labat & Conté 2674 (13); Lewis et al. 755 (9); Louvel 125 (8), 186 (12), 216 (5).

Malcomber 1219 (2), Malcomber et al. 1833 (13); McPherson 14391 (18); Miller 3609 (17); Morat 2306 (20).

Noyes et al. 961 (6), 974 (10), 1028 (13).

Perottet s.n. (12); Perrier de la Bâthie 3513 (13), 3904 (7), 3933 (10), 5270 SF (10); Pervillé s.n. (17).

Rabe 115 (15); Rahajasoa et al. 747 (3); Rakoto 9 (16); Rakotozafy & Raharilala 2189 (17), 2271 (17); Randrianaivo 247 (1), 251 (6), 255 (16); Randriamampionona 438 (6); Randrianasolo & Rasabotsy 32 (7); Ravelonarivo & Rabesaonina 570 (7); Razafimandimbison SG 257 (5), SG 273 (13), SG 352 (10), SG 358 (7), SG 389 (8); Réserves Naturelles: 2751 RN (1), 4905 RN (1), 5152 RN (6), 5524 RN (15), 6234 RN (1), 6257 RN (16), 6809 RN (6), 7822 RN (16), 7906 RN (2), 9002 RN (2), 9045 RN (6), 9052 RN (10), 9129 RN (10), 9229 RN (16), 9453 RN (16), 9982 RN (3), 11089 RN (17), 12975 RN (2).

Schatz et al. 1912 (19), 3858 (3); Scott Elliott 2214 (4); Station Forestière: 841 SF (15), 973 SF (20), 1432 SF (1), 2078 SF (9), 2410 SF (3), 2950 SF (16), 2961 SF (6), 3026 SF (13), 3265 SF (10), 3882 SF (13), 4677 SF (13), 4855 SF (18), 5652 SF (19), 5964 SF (3), 6105 SF (7), 6181 SF (13), 6360 SF (3), 6616 SF (13), 6696 SF (13), 6754 SF (13), 6791 SF (17), 7136 SF (7), 7155 SF (3), 7460 SF (6), 7562 SF (8), 7921 SF (8), 7987 SF (13), 8245 SF (13), 8317 SF (19), 8413 SF (15), 8734 SF (6), 9047 SF (3), 9220 SF (15), 9238 SF (3), 9711 SF (9), 9974 SF (7), 10803 SF (6), 10925 SF (18), 11407 SF (15), 11417 SF (16), 11430 SF (15), 11503 SF (6), 11594 SF (9), 12023 SF (17), 12352 SF (3), 12447 SF (3), 13094 SF (12), 14359 SF (14), 14437 SF (3), 14712 SF (3), 14728 SF (3), 15035 SF (19), 15057 SF (17), 15273 SF (16), 15287 SF (3), 15381 SF (3), 15495 SF (3), 15518 SF (3), 15673 SF (13), 15947 SF (16), 16174 SF (3), 16217 SF (3), 16496 SF (12), 16621 SF (12), 17299 SF (3), 17565 SF (13), 18029 SF (17), 18116 SF (10), 18311 SF (14), 18450 SF (13), 18518 SF (2), 19061 SF (13), 19295 SF (7), 19379 SF (13), 19658 SF (3), 19775 SF (6), 19791 SF (6), 20558 SF (18), 21160 SF (10), 21570 SF (6), 21596 SF (3), 22059 SF (2), 23424 SF (1), 23641 SF (18), 23661 SF (3), 23691 SF (3), 23917 SF (3), 24150 SF (9), 24753 SF (15), 24764 SF (16), 25526 SF (7), 26103 SF (3), 26804 SF (5), 26906 SF (9), 27049 SF (20), 27192 SF (3), 27503 SF (13), 27593 SF (1), 27636 SF (1), 28081 SF (3), 28136 SF (10), 28414 SF (5), 28445 SF (5), 29653 SF (13), 31809 SF (3), 32928 SF (19), 32344 SF (10), 33237 SF (6), 33240 SF (3), 33536 SF (6), 34288 SF (6), 34413 SF (6), 34711 SF (3), 34719 SF (3), S/N SF (3).

Thouvenot s.n. (5), 91 (5), 117 (10); Turk et al. 643 (3).

Ursch s.n. (1).

Villiers et al. 4846 (13); Vigreuse 15418 (3).

Zavah 321-R-107 (19); 5524 RN (?).

Unknown collectors: 12-R-B-172 (5); 14-B-R-230 (9); 86-R-118 (3); 63-R-199 (19); Herbier de la station agricole de l'Alaotra, 2200 (TAN).

CLASSIFICATION, ORIGIN, AND DIVERSIFICATION OF THE NEW ZEALAND HEBES (SCROPHULARIACEAE)[1]

Steven J. Wagstaff,[2] Michael J. Bayly,[3] Philip J. Garnock-Jones,[4] and Dirk C. Albach[5]

Abstract

The New Zealand hebes (Scrophulariaceae) are members of a large Southern Hemisphere clade nested within *Veronica.* Analysis of ITS and *rbc*L sequences suggests that the New Zealand species are derived from a single common ancestor that arrived via long-distance dispersal. After the establishment of this initial founder population in New Zealand, the hebes have undergone at least two major episodes of diversification, giving rise to six clades. The great degree of morphological diversity in the New Zealand hebes contrasts with a corresponding low level of sequence divergence. New Zealand was a source of new emigrants to other regions in the South Pacific that were preadapted to high mountains or forest margins. Our results suggest that two instances of long-distance dispersal from New Zealand to South America, at least one instance from New Zealand to Australia, and one instance from New Zealand to New Guinea have occurred relatively recently. Shorter hops to the Chatham Islands and the subantarctic islands are also supported by the sequence data.

Key words: *Hebe*, ITS, New Zealand, phylogenetic analysis, *rbc*L, Scrophulariaceae, *Veronica.*

Long-distance dispersal has a profound influence on the evolution of insular floras (Carlquist, 1974), and there is substantial evidence suggesting that it occurs relatively frequently (Godley, 1967; Pole, 1994). One of the most remarkable examples of dispersal followed by adaptive evolution on islands is the New Zealand hebes (Scrophulariaceae). Wagstaff and Garnock-Jones (1998, 2000) suggested that the New Zealand hebes are the descendants of a small founder population that may have been derived from a single seed. They proposed that combined influences of inbreeding, genetic drift, and strong selection acting upon small populations have probably played a major role in the rapid diversification of the group.

The hebes are one of the largest and most ecologically diverse plant groups in New Zealand, including over 120 species, with outlier populations in eastern Australia, Tasmania, New Guinea, Rapa Island, and South America. They range from alpine cushion-forming plants (Fig. 5D) to lowland woody shrubs or small trees (Fig. 5M, R, S), and in New Zealand are conspicuous elements in most terrestrial ecosystems except forests and wetlands. Species such as *Hebe armstrongii, H. cupressoides,* and *H. speciosa* have patchy or localized distributions and are considered rare or endangered; about 70% of the species are confined to small regions within New Zealand.

The New Zealand hebes were formerly included in a broadly defined circumscription of the genus *Veronica* (Wettstein, 1891; Cheeseman, 1925), but recent flora and taxonomic treatments (Ashwin & Moore in Allan, 1961; Garnock-Jones, 1993a, b; Heads, 1994a, b) recognize less inclusive groups (see Table 1), usually accepting four genera in New Zealand: *Chionohebe, Hebe, Heliohebe,* and *Parahebe* (Garnock-Jones, 1993a, b). Heads (1987) described an additional genus, *Leonohebe.* Although we do not accept his wide circumscription of that genus, the name *Leonohebe* could be applied to a small clade of four or five species that is supported by the analyses of Wagstaff and Garnock-Jones (1998, 2000).

[1] The authors gratefully acknowledge curators of the experimental gardens and CHR Herbarium at Landcare Research, Lincoln, along with the assistance of Anita Thorne, Andy Glazier, and Elizabeth MacAvoy with the DNA sequencing. Dick Olmstead contributed several of the *rbc*L seqeunces included in our study. Bill Malcolm (Micro-Optics Ltd.) provided many of the photographs, and Alison Kellow assisted with preparation of figures. Earlier versions of this manuscript benefited greatly from the insightful comments of Christine Bezar, Ilse Breitwieser, Mark Chase, Murray Dawson, and Alison Kellow. This research was funded in New Zealand by the Foundation for Research, Science and Technology (contracts C09618 and MNZ601), and the Marsden Fund (contract LAN601).

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Table 1. Classifications of New Zealand hebes. The New Zealand species were placed in three sections of Wettstein's (1891) treatment of *Veronica*, and Cheeseman (1925) placed them in two divisions of *Veronica*.

Wettstein (1891)	Cheeseman (1925)	Ashwin & Moore in Allan (1961)[1]	Heads (1987, 1994b)	Garnock-Jones (1993a, b)
Veronica	***Veronica***			
sect. *Pygmea*	Division *Pygmea*	***Pygmea***	***Chionohebe***	***Chionohebe*** Including *Parahebe* "Group B")
sect. *Hebe*			***Leonohebe***	
			sect. *Densifoliae*	
	Division *Hebe*	***Hebe***		***Hebe***
		"Semiflagriformes"	sect. *Leonohebe*	"Semiflagriformes"
		"Connatae"	sect. *Connatae*	"Connatae"
			sect. *Apiti*	
		"Flagriformes"	sect. *Flagriformes*	"Flagriformes"
			sect. *Aromaticae*	
			sect. *Salicornioides*	
		"Buxifoliatae"	sect. *Buxifoliatae*	"Buxifoliatae"
			Hebe	
		"Subdistichae"	sect. *Subdistichae*	sect. *Subdistichae*
		"Subcarnosae"	sect. *Glaucae*	sect. *Glaucae*
			sect. *Hebe*	sect. *Hebe*
		"Apertae"	ser. *Hebe*	ser. *Hebe*
		"Occlusae"	ser. *Occlusae*	ser. *Occlusae*
			Parahebe	
		"Grandiflorae"		"Grandiflorae"
		"Paniculatae"	sect. *Paniculatae*	***Heliohebe***
sect. *Chamaedrys*	Division *Euveronica*	***Parahebe***		***Parahebe***
		"Group A, B, C"		"Group A, C"
sect. *Labiatoides*	—	—		***Derwentia***
sect. *Paederota*	—	—	—	—
sect. *Paederotoides*	—	—	—	—
sect. *Pseudolysimachia*	—	—	—	—
sect. *Veronicastrum*	—	—	—	—
sect. *Omphalospora*	—	—	—	—
sect. *Beccabunga*	—	—	—	—

[1] In the *Flora of New Zealand* Volume 1 (Allan, 1961), M. B. Ashwin prepared the treatment of *Parahebe*, *Pygmea*, and the informal grouping "Flagriformes" of *Hebe*. The remainder of the *Hebe* treatment, including the informal synopsis, was prepared by L. B. Moore.

This research contributes to ongoing efforts to create a phylogenetic classification of Scrophulariaceae. Olmstead and Reeves (1995) and Olmstead et al. (2001) showed that the Scrophulariaceae, as traditionally circumscribed, are not monophyletic. They identify clades from a dismembered Scrophulariaceae s.l. that could merit formal recognition. In their studies *Veronica* was nested within a large clade they called the Antirrhinaceae *nom. cons. prop.* (Reveal et al., 1999). This large clade was recognized by Olmstead and Reeves (1995) and includes part or all of Bentham's (1876) tribes Digitaleae, Antirrhineae, Cheloneae, and Gratioleae, the small tribe Angelonieae, and the small families Callitrichaceae, Globulariaceae (excluding Selaginaceae), Hippuridaceae, and Plantaginaceae.

The aim of this research is to identify well-supported monophyletic groups among the New Zealand hebes, to improve their classification, infer their origin, and explore underlying processes of diversification. We propose that diversification in the group reflects transoceanic dispersal and adaptive radiation. The hebes have successfully exploited a diversity of ecological niches that were probably created during the recent uplift and glaciation of the mountains of New Zealand.

Materials and Methods

Our sampling strategy capitalized on the unique characteristics of *rbc*L and ITS sequences. The plastid encoded gene *rbc*L has relatively few variable sites, which allowed sequence comparisons among distantly related outgroups, and placement

of the hebes within Scrophulariaceae. It is also useful in that a large number of published *rbc*L sequences are available for comparison (see Chase et al., 1993; Källersjö et al., 1998; Olmstead et al., 2001, and references therein). Finally, Albert et al. (1994) and Bremer and Gustafsson (1997) suggested that the gene *rbc*L approaches clock-like behavior in its evolution, and hence the amount of sequence divergence could be used to estimate divergence times. By comparison, the nuclear encoded ITS-region has many more variable sites than *rbc*L, which provides more informative characters to resolve relationships at lower taxonomic levels (Baldwin et al., 1995).

STUDY GROUP

The *rbc*L study group consisted of 33 species including 12 of the New Zealand hebes with at least 1 representative from each of the currently recognized genera, 5 species of *Veronica*, and 1 species of *Veronicastrum*. Nineteen *rbc*L sequences were newly published herein along with 13 published sequences of Antirrhinaceae from Olmstead et al. (2001), and *Nicotiana tabacum* (Solanaceae) was designated as the outgroup (Lin et al., 1986). Seven sequences were considered redundant; even though they were not identical, the resolution of missing data could potentially make them identical. We therefore excluded *Derwentia derwentiana* and *D. perfoliata*, and the New Zealand accessions of *Hebe elliptica* and *H. salicifolia*, from subsequent analyses. Nineteen of the 37 species included in the *rbc*L analysis were also included in the ITS survey.

The ITS study group included 78 sequences, 19 of which were newly published. Among these are 58 representatives of *Chionohebe*, *Derwentia*, *Heliohebe*, and *Parahebe*, including conspecific accessions of *Chionohebe ciliolata* and *C. densifolia* from Australia and New Zealand, *Parahebe lithophila* from Australia, and *P. vandewateri* from New Guinea. Thirty-five species of *Hebe* were also included, and among these were: at least one representative from each of Moore's (in Allan, 1961) informal groups; *H. formosa* from Tasmania; *H. benthamii* from the New Zealand subantarctic islands; *H. barkeri*, *H. chathamica*, and *H. dieffenbachii* from the Chatham Islands (east of the main islands of New Zealand); accessions of *H. elliptica* from both New Zealand and the Falkland Islands; and *H. salicifolia* from both New Zealand and Chile. *Pseudolysimachion*, *Veronica*, *Veronicastrum*, and *Wulfenia* emerged as potential sister groups of the hebes in the analysis of Hong (1984) and Albach and Chase (2001); therefore a total of 19 species representing these genera were included in our analysis. The Asiatic species *Veronicastrum sibiricum* was designated as the outgroup for the analysis of ITS sequences.

Voucher specimens are listed in Appendix 1, along with collection information, literature citations, and GenBank (<http://www.ncbi.nlm.nih.gov>) accession numbers. The complete data sets are available upon request from the first author, and they were deposited in TreeBASE (<http://www.herbaria.harvard.edu/treebase>). The study accession number is S623, and the matrix accession numbers are M961 (*rbc*L) and M962 (ITS).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from either fresh leaves or leaf fragments dried with silica gel using a modification of the hot CTAB method of Doyle and Doyle (1987). The cpDNA gene *rbc*L and the nrDNA ITS-region [the 3′ end of the 18S rDNA gene; internal transcribed spacer −1 (ITS-1); the 5.8S rDNA gene; internal transcribed spacer −2 (ITS-2); and the 5′ end of the 28S rDNA gene] were amplified by PCR. Primer sequences and our amplification and sequencing techniques follow Olmstead et al. (1992) for *rbc*L, and Wagstaff and Garnock-Jones (1998) for the ITS-region. Excess primers and unincorporated nucleotides were removed from the PCR products by spin column centrifugation (QIAquick PCR purification kit, QIAGEN Inc.). The purified DNA samples were then labeled with Big Dye terminators (PE Applied Biosystems, The Perkin-Elmer Corp.). Both the forward and reverse DNA strands were sequenced by the Waikato University DNA Sequencing Facility. Contig editing and assembly was accomplished using Sequencher version 3.0 (Gene Codes Corp.).

SEQUENCE ALIGNMENT

The sequence alignment for the ITS-region was facilitated by ClustalX (Thompson et al., 1997). A gap penalty setting of 75 and a gap extension penalty of 6.6 were initially used to identify and position large gaps in the sequence data; then low-scoring segments were realigned using a gap penalty setting of 15 and a gap extension penalty of 6.6 with the removing new gaps option turned on. These settings opened and positioned small gaps. The final alignment was inspected and minor revisions were made manually.

Data Analysis

The phylogenetic analyses were accomplished using PAUP* version 4.0d65 (Swofford, 1998). The analyses were conducted using the PAUP* settings random addition sequence with 100 replicates, TBR branch swapping, mulpars in effect, and steepest descent. The characters were all unordered and weighted equally, and gaps were treated as missing data.

Support for the inferred clades is given by jackknife percentages (Farris et al., 1996) and by the number of synapomorphies for each group. Jackknife analysis investigates the structure, or phylogenetic signal, in a matrix without permutation, but excludes an assigned fraction of characters, here set to 30%. The jackknife searches were performed with 1000 replications excluding uninformative sites, maxtrees = 10 for each replication; the starting trees were obtained by random addition with one replication for each jackknife replication, TBR branch-swapping, and mulpars in effect.

The relationship between sequence divergence and time for the gene *rbc*L was discussed by Albert et al. (1994) and Bremer and Gustafsson (1997) and was calculated using the equation:

substitution rate = patristic distance(Dp)/number of nucleotides/inferred time since cladogenesis.

Results

The *rbc*L sequences were 1402 nucleotides in length (positions 27–1428 in tobacco). Among the 1402 sites included in the *rbc*L matrix, 1103 sites were invariant; 144 were parsimony-uninformative, and 155 characters were parsimony-informative. Missing data accounted for 4.7% of the matrix. Most of the missing data fell in a region at the 5′ end of *rbc*L, upstream from the conserved EcoRV restriction site used in cloning some sequences (Olmstead et al., 1992), and in a region downstream from position 1325, the location of a PCR primer site used to amplify some sequences. Most changes (calculated across the maximum parsimony tree shown in Fig. 2) occurred in the third codon position (369); substantially fewer changes occurred in the first (116) and second (47) codon positions. Changes in the third codon position are generally synonymous, and hence are more likely to evolve in a clock-like manner.

The analysis of *rbc*L sequences recovered 9408 maximum parsimony trees distributed in a single island of 529 steps (consistency index = 0.52 excluding uninformative characters, retention index = 0.73); a strict consensus tree is shown in Figure 1, and one of the maximum parsimony trees is shown in Figure 2. Most members of the Antirrhinaceae form a basal grade in our analysis with *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Parahebe*, and *Veronica* forming a clade that receives 100% jackknife support. *V. anagallis-aquatica* is sister to a largely Australasian clade (98% jackknife support) that includes the New Zealand hebes along with *Derwentia*, *Veronica arguta*, and *V. persica*. Relationships within this clade are poorly resolved (Figs. 1, 2).

The mean absolute distance and standard deviation from *Veronicastrum sibiricum* to the *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Parahebe*, and *Veronica* terminals is 29.1 ± 7.7 (see Fig. 2). *Veronicastrum* is reported in the fossil record (Tiffney, 1985) from the mid Miocene some 15 million years before present (mybp). The substitution rate in the *Veronicastrum* lineage was estimated by dividing 29.1 ± 7.7/15 = 1.9 ± 0.5 substitutions for the entire gene *rbc*L. The mean distance from the terminals to the ancestral node of the Australasian species (including *V. persica*, which is Eurasian) is 18.8 changes, which corresponds to an upper Miocene divergence estimate of about 9.9 mybp. The mean distance from the terminals to the ancestral node of the *H. salicifolia* lineage is 7.4 changes, which corresponds to a Pliocene divergence estimate of about 3.9 mybp (Fig. 2).

The aligned ITS matrix was 695 nucleotides in length with gaps created to account for insertions and deletions, among which 364 sites were constant, 109 were parsimony-uninformative, and 222 were potentially parsimony-informative. Missing data accounted for 1.2% and gaps accounted for 9.6% of the ITS data matrix. The 5.8S gene was uniformly 165 nucleotides; ITS-1 varied between 175 and 224 nucleotides and ITS-2 between 203 and 215 nucleotides. Most of the variation in the ITS region was observed in ITS-1 and ITS-2. The 5.8S gene was more conserved. Conserved motifs identified by Liu and Shardl (1994) and Hershkovitz and Zimmer (1996) were identified in the ITS-1 and ITS-2 sequences in our survey.

Thirty-eight insertions and deletions (indels) were inferred in the ITS-1 and ITS-2 spacer regions (Table 2). Mostly these were relatively small, ranging from 1 to 3 bp, but two large insertions of 27 and 44 bp and three deletions of 7 or 8 bp were also inferred. Most of the indels were unique to a single sample, but 13 were shared by two or more species, sometimes uniting groups supported by substitutions in the sequence data alone. Species of *Derwentia* are characterized by a one-base deletion. Species of *Heliohebe* are characterized by a

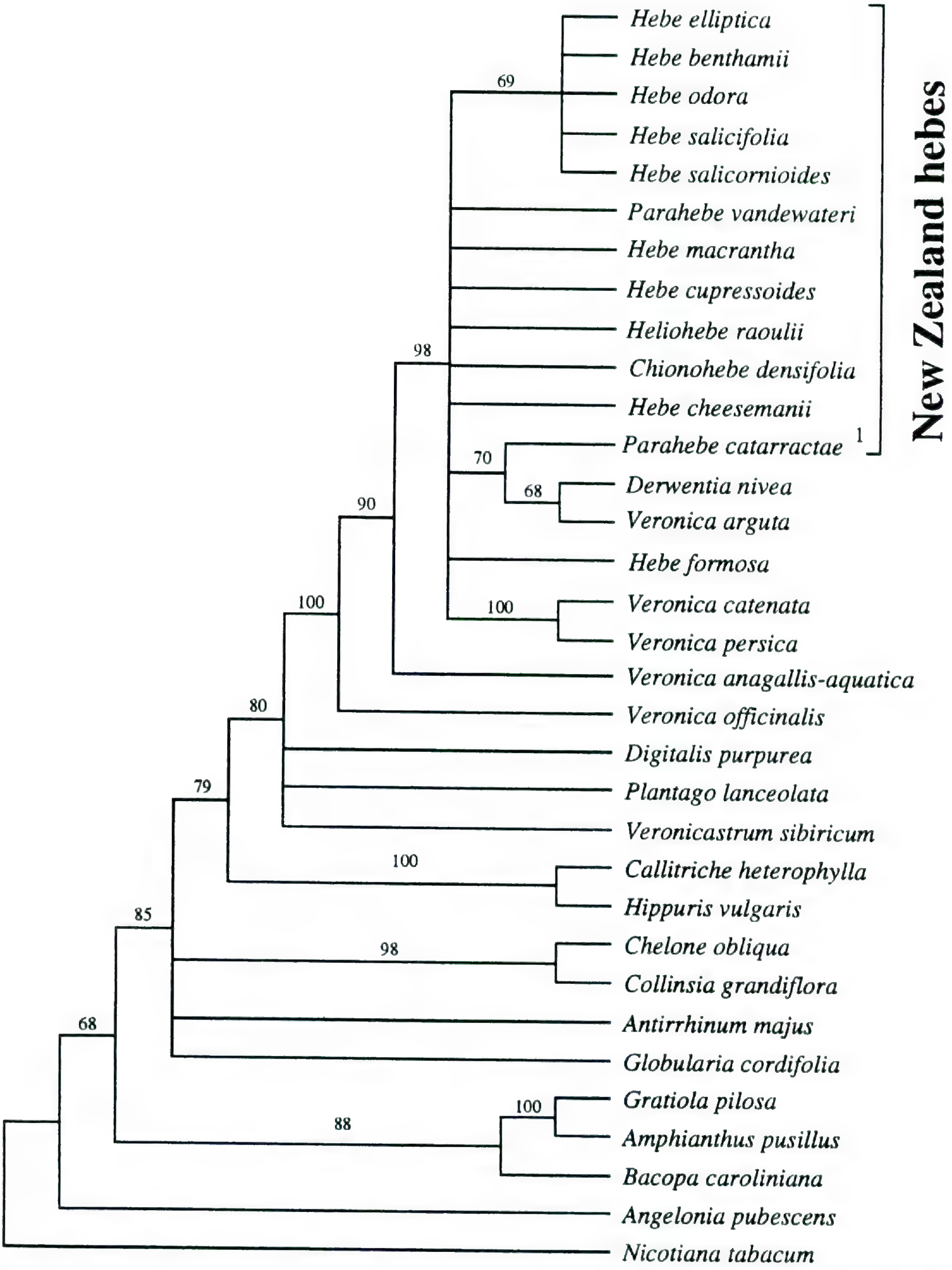

Figure 1. Strict consensus of 9408 minimal length trees produced by parsimony analysis of *rbc*L sequences. This tree shows the placement of New Zealand hebes within the Antirrhinaceae sensu Olmstead et al. (2001), using *Nicotiana tabacum* as an outgroup. Jackknife values > 50% are given above each node.

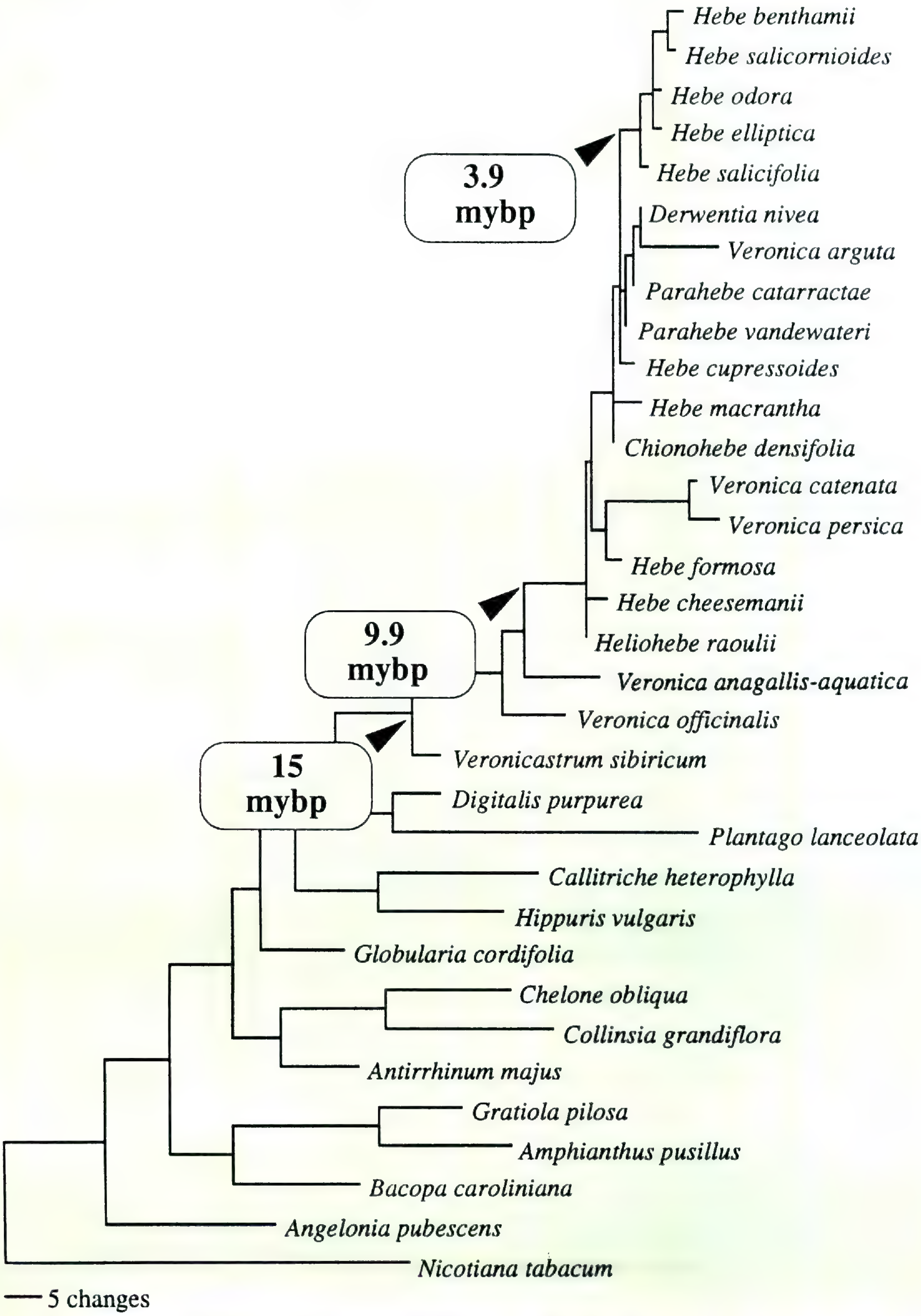

Figure 2. One of the maximum parsimony trees recovered from a parsimony analysis of *rbc*L sequences. The branch lengths are proportional to the number of changes along each branch. See scale at bottom. Fossils of *Veronicastrum sibiricum* are reported from the mid Miocene about 15 mybp. Divergence estimates are provided at the ancestral node of Australasian species (*V. persica* is Eurasian) and the ancestral node of the *Hebe* clade.

Table 2. Insertions and deletions inferred from ITS sequence comparison.

Taxon	Insertion/deletion	Size	Position	Sequence
Veronicastrum sibiricum	Deletion	1	41	t/c
Veronicastrum sibiricum, Wulfenia carinthiaca	Insertion	1	54	c
Veronica glandulosa	Deletion	1	67	t/g
Hebe vernicosa	Insertion	3	68–79	gta
Veronica calycina	Insertion	1	77	t
Veronica chamaedrys	Deletion	1	78	c/g
Veronicastrum sibiricum	Deletion	1	89	c
Wulfenia carinthiaca	Insertion	44	90–134	aatctaggtgtgcaagccccctttgttgagag-tcccgcgcctgctc
Pseudolysimachion spicata, Veronica anagallis-aquatica, V. bellidioides, V. glandulosa, V. glauca, V. officinalis, V. serpyllifolia, V. urticifolia	Insertion	27	108–134	gactagtcgagtgcgccgctctcgctc
Veronica bellidioides, V. officinalis, V. urticifolia	Insertion	1	162	a
Derwentia derwentiana, D. nivea, D. perfoliata, Parahebe lithophila, Veronica arguta	Insertion	1	207	a
Veronica macrostachya	Deletion	3	208–209	cc
Hebe salicifolia	Insertion	1	217	c
Veronica bellidioides, V. glandulosa, V. officinalis, V. urticifolia, Wulfenia carinthiaca	Insertion	1	234	c/g
Veronica persica	Deletion	1	248	a
Veronica chamaedrys, V. anagallis-aquatica	Insertion	1	260	a
Pseudolysimachion spicata, Veronica chamaedrys, V. macrostachya, V. oltensis	Insertion	1	442	a
Veronica urticifolia	Insertion	1	454	c
Veronica anagallis-aquatica	Insertion	1	467	t
Pseudolysimachion spicata, Veronica anagallis-aquatica, V. bellidioides, V. fruticulosa, V. glandulosa, V. glauca, V. officinalis, V. saturejoides, V. serpyllifolia, V. urticifolia, Veronicastrum sibiricum, Wulfenia carinthiaca	Deletion	1	474	g
Parahebe canescens	Insertion	1	475	g
Veronica bellidioides	Insertion	2	501	cc
Wulfenia carinthiaca	Deletion	1	503	t
Heliohebe hulkeana, H. lavaudiana, H. raoulii	Insertion	1	508	t
Veronica persica	Deletion	1	573	t
Hebe elliptica, H. elliptica, Parahebe birleyi, P. brevistylis, P. decora, P. lyallii, P. spathulata, P. vandewateri	Deletion	8	583–590	tctcgtgc
Parahebe planopetiolata	Deletion	7	590–596	catctcc
Parahebe canescens	Deletion	8	591–598	atctccgc
Veronica persica	Deletion	3	592–594	tca
Heliohebe hulkeana, H. lavaudiana, H. raoulii	Deletion	1	606	g
Parahebe vandewateri	Deletion	1	609	a
Veronica chamaedrys	Deletion	2	609–610	ag

Table 2. Continued.

Taxon	Insertion/ deletion	Size	Position	Sequence
Parahebe canescens	Insertion	3	615–616	cat
Veronica chamaedrys	Deletion	2	620–621	tc
Pseudolysimachion spicata	Deletion	2	625–626	ac
Veronica chamaedrys, V. serpyllifolia	Insertion	1	631	a
Veronica austriaca, V. oltensis	Insertion	2	638–639	gc
Veronica arguta	Insertion	1	640	c

one-base insertion and a one-base deletion. Both accessions of *Hebe elliptica* and nine species of *Parahebe* have an eight-base deletion that appears to have evolved independently at least three times (Table 2). This deletion is lacking in *Parahebe linifolia* and in *P. catarractae* subsp. *catarractae* and subspecies *martinii*. The South American accession of *Hebe salicifolia* has a unique one-base insertion that is lacking in the accession of *Hebe salicifolia* from New Zealand.

The ITS sequences in our study were evolving at a faster rate than *rbc*L. The average rate of change per variable site for *rbc*L was 1.7 (tree length of 532/number of variable sites 144 + 155). The aligned ITS sequences were shorter than *rbc*L, there were more variable sites (331), and the average rate of change per variable site was 3.6 for the ITS region.

Parsimony analysis of the ITS-region recovered 6931 maximum parsimony trees distributed in at least two islands of 1213 steps (consistency index = 0.41 excluding uninformative characters, retention index = 0.73); a strict consensus tree is shown in Figure 3 and one of the maximum parsimony trees in Figure 4. Based upon the results from analysis of *rbc*L sequences (Figs. 1, 2), *Veronicastrum sibiricum* was designated as the outgroup. The earliest divergence within the ingroup is between *Wulfenia carinthiaca* and all other taxa. The Northern Hemisphere species of *Veronica* are found in five clades that form a grade basal to a Southern Hemisphere clade comprising the New Zealand hebes and their relatives. A heterogeneous Australian clade comprised of *Derwentia, Hebe formosa, Parahebe lithophila, Veronica arguta,* and *V. calycina* (82% jackknife; 18 synapomorphies) is sister to the New Zealand hebes, though there is relatively little support for this relationship (70% jackknife; 10 synapomorphies) (Figs. 3, 4).

Six well-supported clades are identified among the New Zealand hebes, but the relationships among these clades are unclear (Figs. 3, 4). The first is a clade that comprises *Leonohebe* s. str. including a well-supported group, *Hebe tetrasticha, H. cheesemanii,* and *H. ciliolata* (99% jackknife; 6 synapomorphies) with *Hebe cupressoides* weakly supported as their sister (61% jackknife; 3 synapomorphies). The *Chionohebe* A clade (98% jackknife; 5 synapomorphies) includes *Parahebe planopetiolata* and the cushion-forming species of *Chionohebe* with both the New Zealand and Australian accessions of *C. ciliolata*. The *Chionohebe* B clade consists of *Parahebe trifida* and both the New Zealand and Australian accessions of *Chionohebe densifolia* (91% jackknife; 4 synapomorphies). The fourth clade includes 6 species of *Parahebe* (93% jackknife; 7 synapomorphies) and accommodates the informal "Groups A & C" of Ashwin (in Allan, 1961; Table 1) and *P. spathulata*. The fifth clade includes all the species of *Heliohebe* in our analysis (100% jackknife; 13 synapomorphies). The sixth includes the remaining species of *Hebe* with both New Zealand and South American accessions of *Hebe salicifolia* and *Hebe elliptica* (100% jackknife; 11 synapomorphies). *Hebe macrantha* is weakly supported as the sister to the rest of this clade (50% jackknife; 4 synapomorphies) (Figs. 3, 4).

Discussion

Large, unwieldy genera with a cosmopolitan distribution such as *Veronica* pose among the most difficult taxonomic problems for plant systematists, whose opinions are often strongly held. One of the most vexing of these problems is the inconsistent means by which taxonomists define generic boundaries and the recognition of rank within a hierarchical classification scheme. Recent taxonomic treatments in the Southern Hemisphere have favored narrow circumscriptions, and several new genera have been segregated from *Veronica* (see Table 1), whereas taxonomists in Europe and North America have traditionally embraced a broad ge-

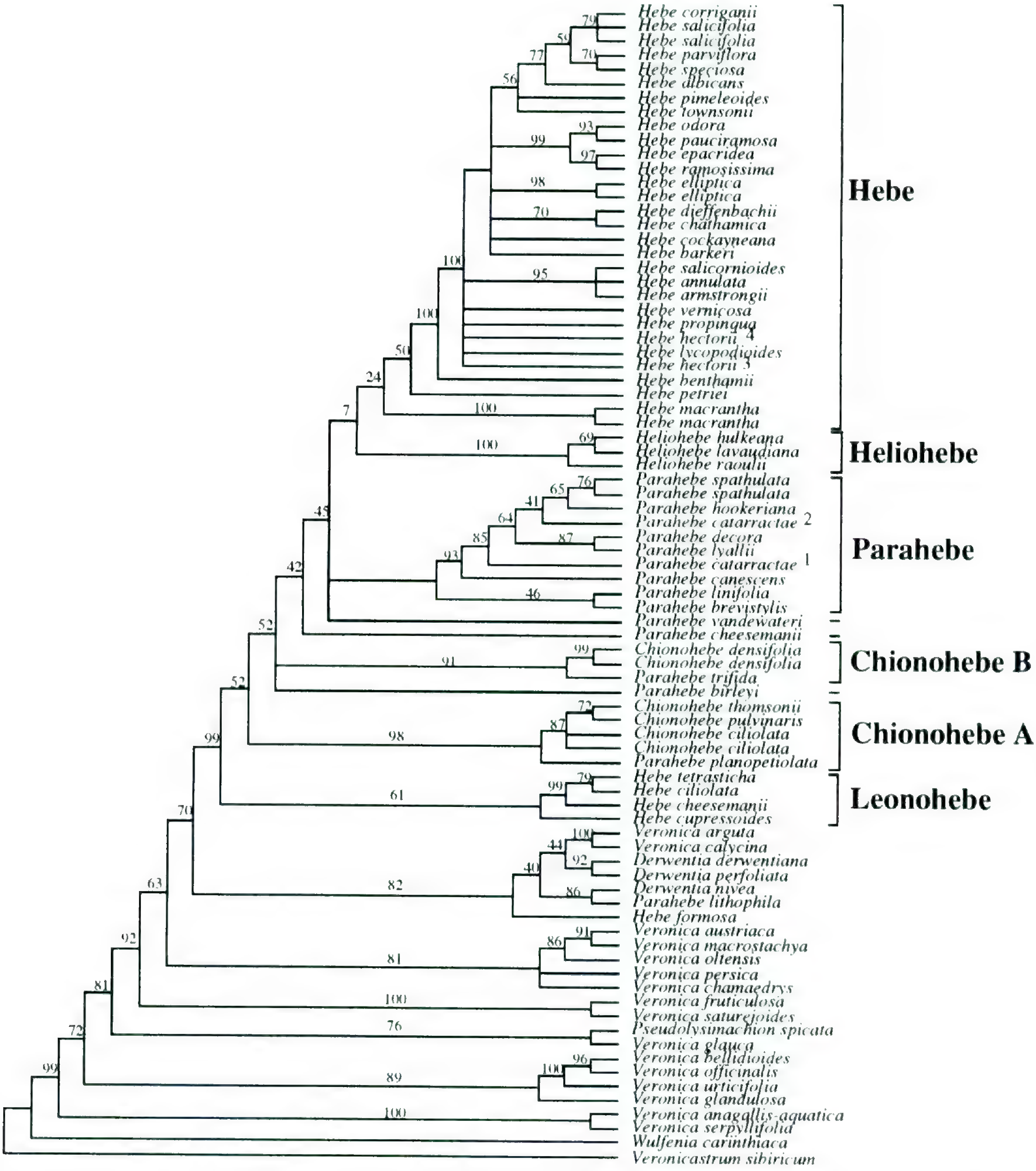

Figure 3. Strict consensus of 6931 minimal length trees produced by parsimony analysis of the entire ITS-region. Notable clades are identified with brackets. Jackknife values > 50% are given above each node. [1]*Parahebe catarractae* subsp. *martinii*, [2]*Parahebe catarractae* subsp. *catarractae*, [3]*Hebe hectorii* subsp. *subsimilis*, [4]*Hebe hectorii* subsp. *hectorii*.

neric definition of *Veronica*, e.g., Wettstein (1891). This discrepancy of opinion contributes to taxonomic ambiguity and instability.

Our results support those of Albach and Chase (2001), implying that the genus *Veronica* is at best paraphyletic by exclusion of the Southern Hemisphere genera *Chionohebe*, *Derwentia*, *Hebe*, *Heliohebe*, *Leonohebe*, and *Parahebe* (Figs. 1, 3), as well as the Eurasian genera *Paederota* and *Pseudolysimachion*, and the North American genera *Synthyris* and *Besseya*. One possible solution is to lump them all in a broad circumscription of *Veronica*. This move, however, would create a cascade of nomenclatural changes requiring the recognition of many new combinations and the adoption of old combinations within *Veronica*. We

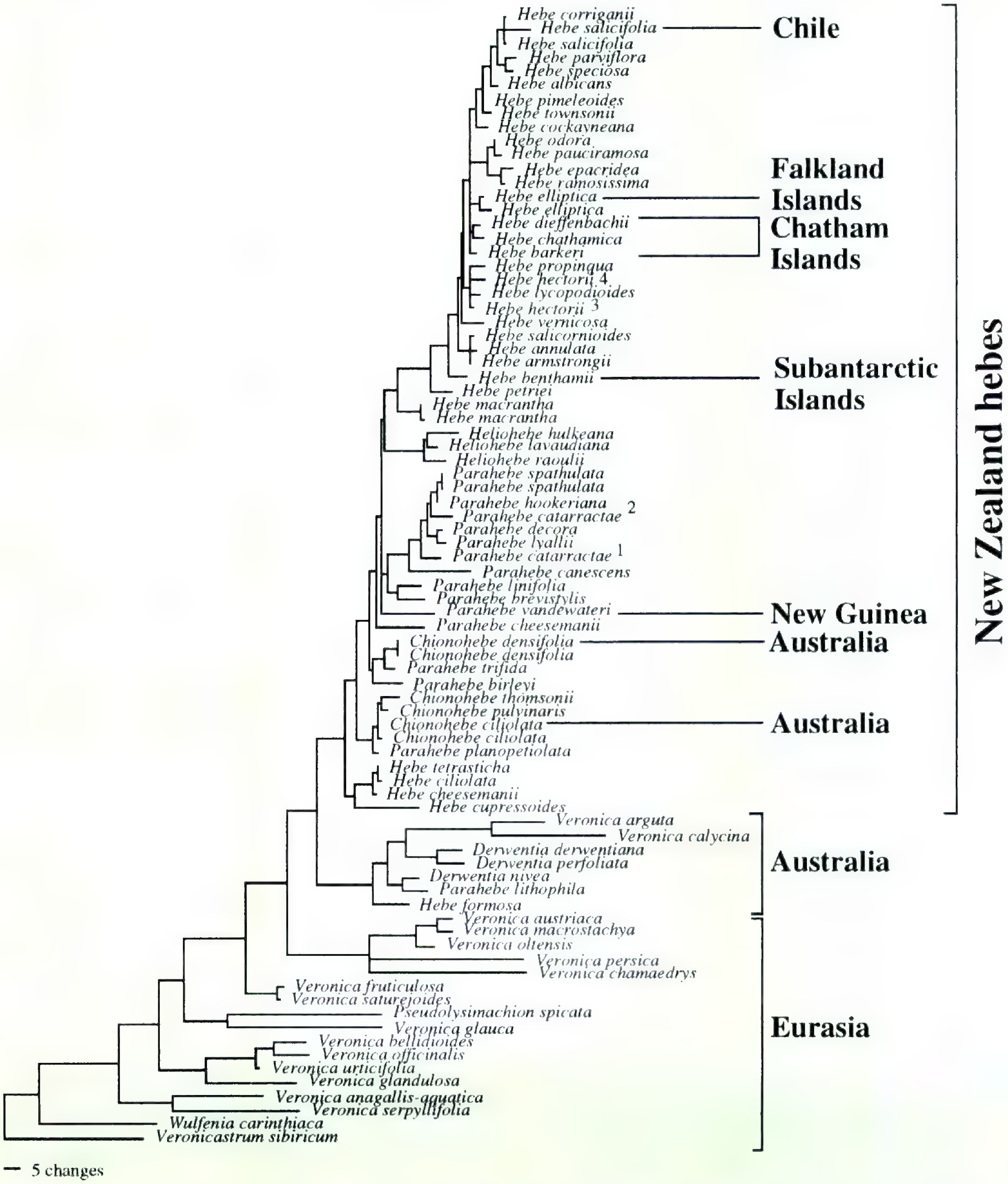

Figure 4. One of the maximum parsimony trees recovered from a parsimony analysis of the ITS-region. The New Zealand hebes comprise a well-supported monophyletic group with outliers on the offshore islands and in Australia, New Guinea, and South America. Dispersal away from the main islands of New Zealand is inferred in nine species. Branch lengths are proportional to the number of changes along each branch. See scale at bottom. [1]*Parahebe catarractae* subsp. *martinii*, [2]*Parahebe catarractae* subsp. *catarractae*, [3]*Hebe hectorii* subsp. *subsimilis*, [4]*Hebe hectorii* subsp. *hectorii*.

accept that retaining a paraphyletic *Veronica* obscures phylogenetic relationships; however, an alternative approach is to recognize smaller, less inclusive clades as generic segregates of *Veronica*. This approach was adopted by Hong (1984). Here we identify major clades supported by the DNA sequences and describe patterns of diversification in the New Zealand hebes.

MAJOR CLADES OF NEW ZEALAND HEBES

A heterogeneous clade composed of *Derwentia*, *Hebe formosa*, *Parahebe lithophila*, *Veronica arguta*,

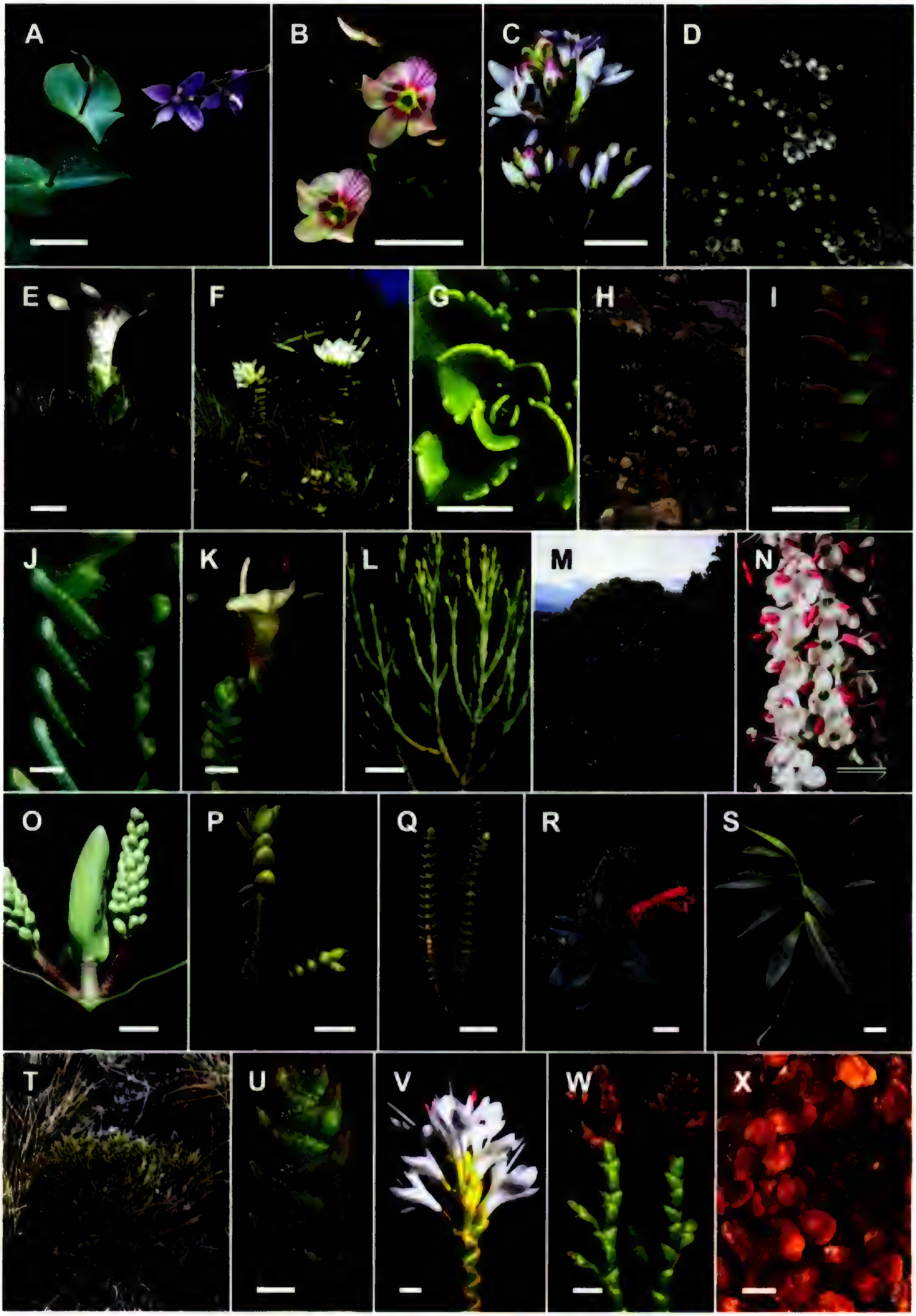

Figure 5. Plate illustrating some of the morphological diversity in the New Zealand hebes. —A. Flowering shoot of *Derwentia perfoliata* with toothed leaves obscure in this picture. —B. Flowers of *Parahebe catarractae*. —C. Paniculate and terminal inflorescence of *Heliohebe raoulii* subsp. *maccaskillii*, *P. J. Garnock-Jones 2123*. —D. Cushion habit

and *V. calycina* is sister to the New Zealand hebes (Figs. 3, 4). The genus *Derwentia* includes nine currently accepted species that are endemic to Australia, from southeastern Queensland to Tasmania and west to Kangaroo Island in South Australia, where they are found mostly in tableland or cool temperate regions (Briggs & Ehrendorfer, 1992). Toothed leaves [only on the lower branches of *H. formosa* and often obscure in *D. perfoliata* (Fig. 5A)], and a dense ring of hairs in the corolla throat (glabrous in *H. formosa*) are possible synapomorphies that unite the clade. *Derwentia* and *Hebe formosa* also have similar growth forms; their new shoots are initiated at the base of the plant, overtopping older, short-lived branches. *Hebe formosa* is distinguished from *Derwentia* by the occurrence of a one-base insertion (Table 2). The chromosome number of *Hebe formosa* is $n = 21$, this possibly being the ancestral state within the *Derwentia* clade; chromosome numbers of $n = 19$ or 20 are published for *Derwentia* (Briggs & Ehrendorfer, 1992).

We identify six major clades within the New Zealand hebes that are supported by the sequence data, which we refer to as the *Leonohebe* clade, the *Chionohebe* A clade, the *Chionohebe* B clade, the *Parahebe* clade, the *Heliohebe* clade, and the *Hebe* clade (Fig. 3). ITS sequences provide strong support for the *Leonohebe* clade (Figs. 3, 4), comprising *Hebe cheesemanii* (Fig. 5K), *H. ciliolata* (Fig. 5J), and *H. tetrasticha*. *Hebe cupressoides* (Fig. 5L) is weakly supported as sister to this clade. These species are endemic to the South Island of New Zealand. They have traditionally been included in *Hebe*, but here, as in previous analyses (Wagstaff & Garnock-Jones, 1998, 2000), are far removed from the other species that Moore (in Allan, 1961) included in that genus. *Hebe cupressoides* and members of the *Leonohebe* clade lack the dorsal capsule compression typically found in members of *Hebe*, and a potential synapomorphy for the group is possession of a distinctive cupressoid growth habit, which has apparently evolved independently from that in the whipcord hebes [e.g., *H. annulata*, *H. armstrongii*, *H. hectorii*, *H. lycopodioides*, *H. propinqua*, and *H. salicornioides*, which have a similar growth form (Figs. 5T–W)]. *Hebe cheesemanii*, *H. ciliolata*, and *H. tetrasticha*, along with *H. tumida*, comprise the informal group "Semiflagriformes" of Moore (in Allan, 1961). These similar species are subshrubs that occur in rocky areas at high altitude and are characterized by possession of lateral inflorescences (Fig. 5K), dioecious breeding system, and sour-scented flowers. We refer to this group as the *Leonohebe* clade, because *Leonohebe ciliolata* (*H. ciliolata*) was designated as the nomenclatural type for that genus by Heads (1987). If the group, including *H. cupressoides*, is treated as generically distinct from *Hebe* (and other genera of the *Hebe* complex; see Garnock-Jones, 1993a), then the use of the name *Leonohebe* seems warranted, though this is a much more restricted use of the name than the clearly polyphyletic circumscription originally employed by Heads (1987).

The *Chionohebe* A clade encompasses the cushion-forming species of *Chionohebe*. All of these species occur in the South Island where they are high-alpine plants of rock and scree. The cushion-forming species

←

of *Chionohebe thomsonii*, male plant, Eyre Mts., South Island, *P. J. Garnock-Jones 1906*. —E. Lateral view of erect tubular flower of *Chionohebe pulvinaris*, from Takitimu Range, South Island. F, G. *Hebe macrantha* var. *brachyphylla*. —F. Habit of a plant ca. 15 cm tall from same population as *M. J. Bayly 560*, Mt. Arthur, South Island. —G. Apex of vegetative shoot from Mt. Arthur, WELT 82554. H, I. *Hebe epacridea*. —H. Habit of a plant ca. 10 cm tall, same population as *M. J. Bayly 795*, Mt. St. Patrick, South Island. —I. Branchlet of plant from unknown locality. —J. *Hebe ciliolata*, branchlet showing ciliolate leaf margins, plant from Mt. Arthur, WELT 82556. —K. *Hebe cheesemanii*, male plant, from same population as *M. J. Bayly 756–757*, Black Birch Ra., South Island. —L. *Hebe cupressoides*, branchlet, cultivated Atawhai, Nelson, South Island, WELT 82553. M, N. *Hebe parviflora*. —M. Habit of a plant ca. 2.5 m tall from same population as *P. J. Garnock-Jones 2258*. Hauhangaroa Ra., North Island. —N. Inflorescence, *P. J. Garnock-Jones 2257*. O, P. *Hebe albicans*. —O. Shoot apex showing young lateral inflorescences and large apical vegetative bud, from Mt. Arthur, South Island, WELT 82555. —P. Shoot of plant from Cobb Valley, South Island, *M. J. Bayly S-31*. —Q. *Hebe pauciramosa*, shoot of plant from Mt. Brewster, South Island, *M. J. Bayly 1478*. —R. *Hebe speciosa*, shoot from a plant cultivated at Otari-Wiltons Bush, Wellington, originally from Maunganui Bluff, North Island. —S. *Hebe salicifolia*, shoot of plant from Upper Wairau Valley, South Island, *M. J. Bayly S-70*. T–V. *Hebe lycopodioides* subsp. *lycopodioides*. —T. Habit of plant from same population as *M. J. Bayly 1512*, Mt. Nimrod, South Island. —U. Apical portion of vegetative branchlet, cultivated in Landcare Research Gardens, Lincoln, originally from Fish Lake, Tarndale, South Island, WELT 82551. —V. Terminal inflorescence of a plant from same population as *M. J. Bayly 771–773*, Lake Tennyson, South Island. —W. Branchlets of *Hebe armstrongii* showing terminal infructescences, cultivated in Landcare Research Gardens, Lincoln, originally from Nigger Stream, Canterbury, South Island, WELT 82552. —X. Small, light seeds of *Hebe elliptica* (typical of those of most *Hebe*), cultivated, Otari-Wiltons Bush, Wellington, North Island. Scale bars: A, B, = 1 cm; C, G, I, L, N = 5 mm; E, V, W = 2 mm; J, K, U, X = 1 mm; O, P, Q, R, S = 2 cm.

of *Chionohebe* (e.g., Fig. 5D) are united by several synapomorphies, including cushion habit with the decussate leaf pairs slightly offset to form a pseudospiral (Heads, 1994b), thick-walled bristle-like eglandular hairs, solitary flowers with erect long corolla tubes (e.g., Fig. 5E), and corolla veins branching distally in the tube (Garnock-Jones, 1993a). The *Chionohebe* A clade is sister to *Parahebe planopetiolata*, one of the species of *Parahebe* "Group B" of Ashwin (in Allan, 1961). With *Parahebe planopetiolata* they share a five-lobed corolla and hygrochastic capsule dehiscence, but the species in the *Chionohebe* B clade also have these features.

The *Chionohebe* B clade includes *C. densifolia* (Australian and New Zealand populations), plus *Parahebe trifida* from the informal *Parahebe* "Group B" of Ashwin (in Allan, 1961) (Figs. 3, 4). *Parahebe birleyi* is not included in this clade in all trees, and in the consensus tree forms a polytomy with it and several other clades in the complex. The species of the *Chionohebe* B clade are all alpine plants found in the southern region of the South Island. *Parahebe trifida* occurs in alpine flushes and snowbanks, *P. birleyi* is a plant of nival rock ledges, and *C. densifolia* is found in a range of stony alpine habitats. *Chionohebe densifolia* is also found in the Kosciusco National Park in Australia. *Chionohebe densifolia*, *P. trifida*, and *P. birleyi* are all similar in appearance. Several of their shared characters are likely to be synapomorphies, including few-flowered inflorescences, large flowers with purple anthers, and presence of long glandular hairs on leaves. Other shared characters are also shared with the *Chionohebe* A clade, including old leaves withering and fading but retained on stems. All three species of the *Chionohebe* B clade are thought to form hybrids with cushion-forming species of *Chionohebe* A clade (Wagstaff & Garnock-Jones, 2000). There is little evidence from morphology to separate the *Chionohebe* A and B clades. Garnock-Jones (1993a), from a cladistic analysis of morphological and flavonoid data, proposed a more inclusive "*Chionohebe*" clade incorporating all the species of *Chionohebe* and *Parahebe* "Group B" of Ashwin (in Allan, 1961). Such a grouping appears paraphyletic at best in this and earlier ITS studies (Wagstaff & Garnock-Jones, 2000).

The *Parahebe* clade includes all the representatives of the informal *Parahebe* "Group A" of Ashwin (in Allan, 1961) plus *P. spathulata*. *Parahebe spathulata* is anomalous in this clade, which otherwise has morphological support from inflorescence, floral, and flavonoid characters (Garnock-Jones, 1993a). A sister relationship between this clade and *P. canescens*, the sole species of Ashwin's "Group C," has 93% jackknife support. The informal "*Parahebe* Groups A and C" share several floral apomorphies (Garnock-Jones, 1993a). *Parahebe brevistylis* and *P. linifolia* (from Ashwin's "Group B") form a weakly supported small clade, which is sister to the "Group A and C" species. The clade is represented in both the North and South Islands of New Zealand, where species occur in well-drained soils associated with river banks, cliffs, and screes. *Parahebe canescens* is a creeping diminutive herb of South Island lake shores; its reduced features match convergent similarities seen in other plants associated with this habitat. The entire clade except for *P. brevistylis* and *P. spathulata* is united by floral features such as short corolla tubes, colored nectar guides (Fig. 5B), and stamen filaments narrowed at the base. In the case of *P. brevistylis*, the differences can be explained as losses of adaptations for insect pollination (Garnock-Jones, 1976b). *Parahebe spathulata* shares some features of habit and flower morphology with *P. cheesemanii* and might have an allopolyploid origin involving species from the *Parahebe* clade and the *P. cheesemanii* lineage.

The *Heliohebe* clade (Figs. 3, 4) was formerly recognized as *Hebe* "Paniculatae" in the informal classification of Moore (in Allan, 1961), and later segregated as a distinct genus by Garnock-Jones (1993b) (Table 1). It was also previously recognized as a distinct group in the key of Cheeseman (1925). *Heliohebe* includes five species that are found in northeastern parts of the South Island on rock outcrops, cliffs, and sometimes in grassland. Monophyly is well supported by two unique indels and several possible morphological apomorphies including an inflorescence that is a terminal, compound raceme or spike (Fig. 5C), protogyny (also evident in Fig. 5C, where styles are protruding from buds on the lowest inflorescence branches), stamens erect, anthers cream or yellow, seeds fusiform to irregular in shape and winged, and hemitropous ovules (Garnock-Jones, 1993b).

The *Hebe* clade corresponds to *Hebe* sensu Moore (in Allan, 1961) with the exclusion of *Heliohebe* and members of the *Leonohebe* clade. The majority of species within the *Hebe* clade form a well-supported group (100% jackknife value), with weaker support for *Hebe macrantha* (Fig. 5F, G) and *H. petriei* as sisters to this group (Figs. 3, 4). The *Hebe* clade is largely endemic to New Zealand, including many of its surrounding islands, with two species also extending to South America, and one species (*H. rapensis*, not included in this analysis) endemic to Rapa Island (Fig. 6). The clade is large and morphologically diverse; unambiguous morphological

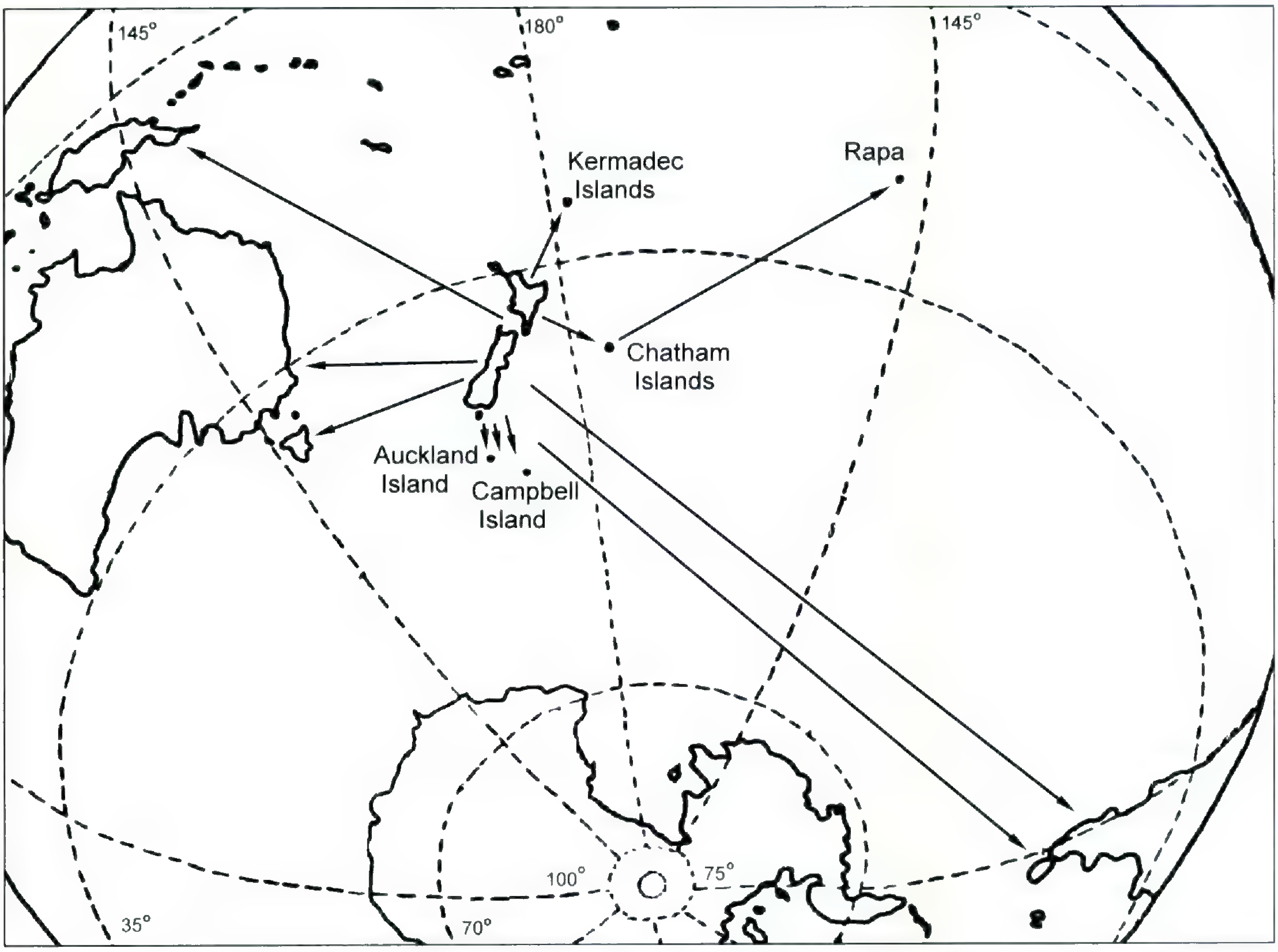

Figure 6. Map showing postulated dispersal of hebes from the main islands of New Zealand.

synapomorphies are difficult to identify, with absences or reversals in some taxa. Wagstaff and Garnock-Jones (1998) suggest that synapomorphies may include: a shrubby or arborescent habit (e.g., Fig. 5M, R, S), large leaf bud (e.g., Fig. 5O), entire leaf margins, protandrous flowers, peltate placentas, acute capsule apices, 3/5 or 5/8 inflorescence phyllotaxis. Within the *Hebe* clade there is little resolution, but several relationships are worthy of note. Firstly, the "Connatae" of Moore [in Allan, 1961, represented by *H. benthamii*, *H. petriei*, *H. epacridea*, (Fig. 5H, I) and *H. ramosissima*] are polyphyletic, with some members closely related to "Buxifoliateae" (*H. odora* and *H. pauciramosa*). These relationships were first suggested by Wagstaff and Garnock-Jones (1998), and the addition of further taxa in this study continues to support this earlier assessment. Secondly, as found by Wagstaff and Wardle (1999), three of the cupressoid species, *H. salicornioides*, *H. armstrongii* (Fig. 5W), and *H. annulata* (which share possession of fused anterior calyx lobes and chromosome number of $n = 21$), form a well-supported clade. Thirdly, two of the Chatham Island endemics, *H. chathamica* and *H. dieffenbachii*, are sister species (Figs. 3, 4), with the third Chatham Island endemic, *H. barkeri*, being placed in a large polytomy that includes this grouping. *Hebe macrantha*, placed with weak jackknife support at the base of the *Hebe* clade, lacks many of the previously mentioned synapomorphies for the group. This species has long held an isolated or ambiguous position, being placed by Moore (in Allan, 1961) in its own grouping, *Hebe* "Grandiflorae," and was included in *Parahebe* by Heads (1987, 1994b). For the present we suggest its retention in *Hebe*, which still leaves the genus, with the exclusion of *Heliohebe* (Garnock-Jones, 1993b) and the *Leonohebe* clade, monophyletic (see Table 1).

TAXA OF UNCERTAIN AFFINITIES

Many of the genera and subgeneric groupings historically recognized in the *Hebe* complex (e.g., *Heliohebe*, cushion-forming species of *Chionohebe*, and some *Hebe* groups) are shown to be monophyletic in this study. Significant exceptions are *Parahebe* "Group B" (of Ashwin in Allan, 1961) and species groups within *Hebe* [e.g., sects. *Hebe*, *Sub-*

distichae, *Glaucae*, and the informal group "Connatae" of Moore (in Allan, 1961)] (see Table 1).

The species of *Parahebe* "Group B" are widely scattered, forming a grade among the New Zealand hebes, and few show any close relationship to other members within their informal group. Previous authors (Ashwin in Allan, 1961; Garnock-Jones, 1976b, 1993a) have suggested the *Parahebe* "Group B" species exhibit considerable morphological similarity, but now it seems this similarity might derive from plesiomorphic character states (relative to the *Hebe–Heliohebe* clade), from convergent evolution of floral features associated with self-pollination (Garnock-Jones, 1976b), and perhaps from reticulate evolution in *P. spathulata* (discussed above). Garnock-Jones (1993a) suggested that *Parahebe* "Group B" and *Chionohebe* should be united, but this view receives no support from the ITS analyses (Wagstaff & Garnock-Jones, 2000, and herein). Wagstaff and Garnock-Jones (2000) inferred that the ancestors of *Parahebe* and *Chionohebe* initially evolved in a montane or alpine environment, then subsequently radiated into lowland environments during episodes of Pleistocene glaciation. Extinction probably had a more profound effect on the basal lineages of *Parahebe* and *Chionohebe*, and this process further confounds our efforts to resolve relationships.

The relationships among species of *Hebe* remain uncertain after ITS analyses (Figs. 3, 4). Branch lengths are too short for us to confidently derive an infrageneric classification from this study. It may be that speciation and diversification in the *Hebe* clade is too recent for ITS divergence to reveal its phylogenetic pattern. Reticulate evolution might also have clouded the molecular signal either through diploid hybrid speciation or allopolyploidy in this group where about 32% of the species are polyploid.

ORIGIN, DIVERSIFICATION, AND DISPERSAL

Two widely differing opinions have been presented regarding the age and origins of the New Zealand hebes. Some authors (e.g., Skipworth, 1973; Heads, 1994a) have proposed a Gondwanan origin to account for the present distribution of the group, whereas others (e.g., Raven, 1973; Garnock-Jones, 1993a; Wagstaff & Garnock-Jones, 1998) have suggested the group has arrived more recently in the Southern Hemisphere and that dispersal has played an important role in shaping its distribution. The data presented here lend support to the latter proposition.

A primary contribution of the present work is its assessment of relationships between *Veronica* and Australasian members of the *Hebe* complex. Although a close relationship between these two groups has long been assumed on morphological grounds (e.g., Wettstein, 1891; Cheeseman, 1925; Raven, 1973), some authors (e.g., Hong, 1984) have directly opposed the notion that Australasian taxa are derived directly from within *Veronica*. Our analysis of *rbc*L clearly supports a close relationship of *Veronica* to the Australasian genera, with the strict consensus including a well-supported (100% jackknife) *Hebe–Veronica* clade (Fig. 3). Analysis of ITS sequences shows the Australasian members to form a clade nested within a paraphyletic *Veronica*. This pattern of relationships is congruent with the notion that the *Hebe* complex is an Australasian radiation of *Veronica*.

Our assessment of the time frame for the origin and radiation of the Australasian genera, and the New Zealand hebes in particular, relies on inferences from the fossil record, the geological and climatic history of New Zealand, and the distributions and ecological tolerances of extant species. For *Hebe*, the earliest appearance in the fossil record is in the Pliocene (Mildenhall, 1980), for Scrophulariaceae it is in the mid Miocene (Tiffney, 1985), and for the whole of the Lamiales (sensu APG, 1998) it is in the mid Eocene (Muller, 1981). Although there is always the possibility that older fossils will be found, it would be inconsistent with this record to assume that divergence, either within the Australasian *Hebe* complex, or between members of that group and *Veronica*, occurred in Gondwanan (Cretaceous) or earlier times.

We acknowledge that the divergence estimates presented in Figure 2 are crude and await further refinement. The paucity of the fossil record and the occurrence of undetected multiple substitutions on

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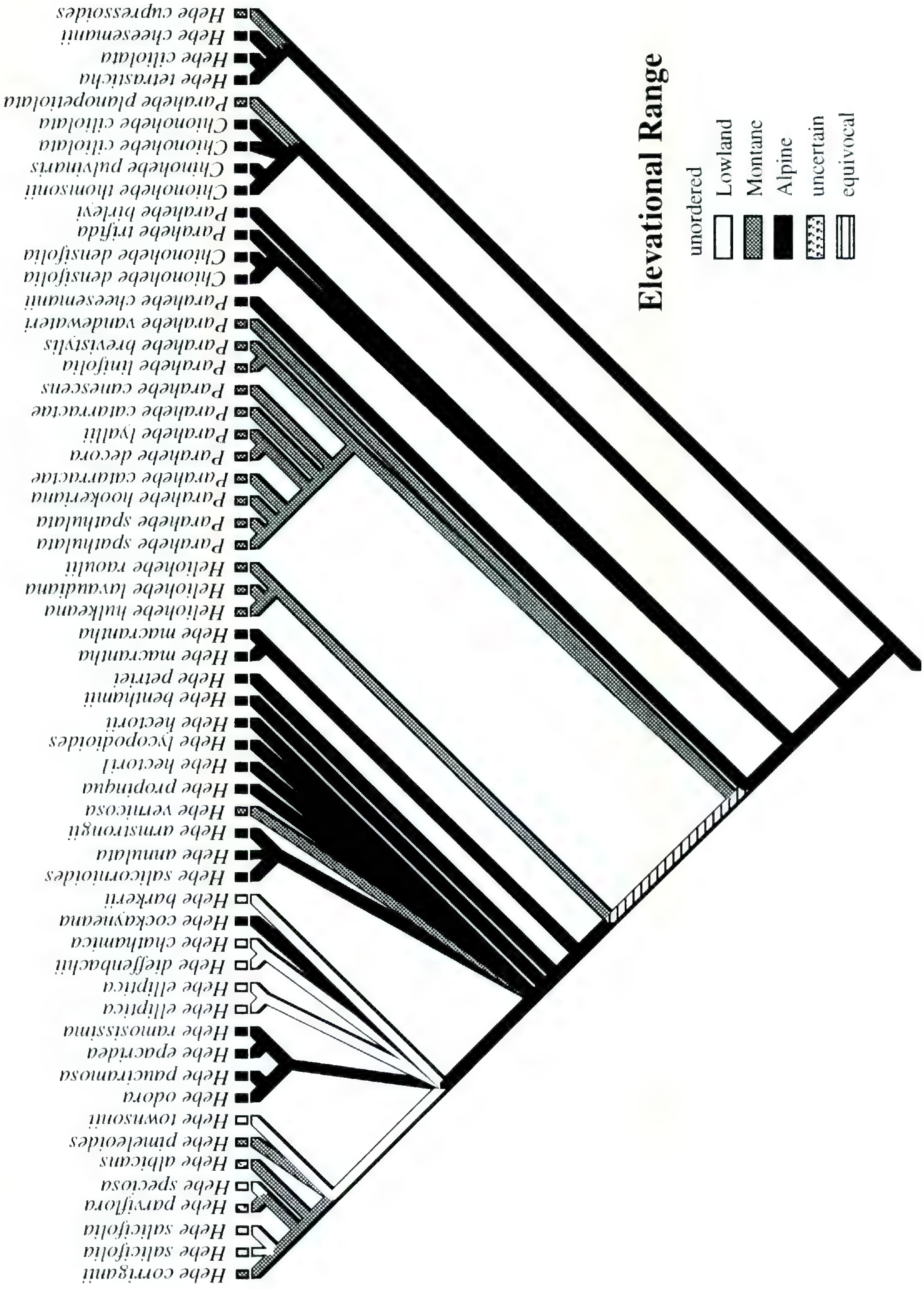
Figure 7. Details of the natural elevational range of species of New Zealand hebes, overlaid on the strict consensus of trees produced by analysis of ITS sequences. Species are regarded as alpine if they occur predominantly in areas above the natural tree line. The other two elevational zones are less precisely defined with, on the two main islands of New Zealand, lowland corresponding to those areas below ca. 500 m above sea level, and montane being those between ca. 500 m and up to ca. 1000 m (but below natural tree line). Members of the basal grade of New Zealand hebes all occur in alpine or montane environments.


Elevational Range
unordered
Lowland
Montane
Alpine
uncertain
equivocal
Hebe corriganii
Hebe salicifolia
Hebe salicifolia
Hebe parviflora
Hebe speciosa
Hebe albicans
Hebe pimeleoides
Hebe townsonii
Hebe odora
Hebe pauciramosa
Hebe epacridea
Hebe ramosissima
Hebe elliptica
Hebe elliptica
Hebe dieffenbachii
Hebe chathamica
Hebe cockayneana
Hebe barkeri
Hebe salicornioides
Hebe annulata
Hebe armstrongii
Hebe vernicosa
Hebe propinqua
Hebe hectorii
Hebe lycopodioides
Hebe hectorii
Hebe benthamii
Hebe petriei
Hebe macrantha
Hebe macrantha
Heliohebe hulkeana
Heliohebe lavaudiana
Heliohebe raoulii
Parahebe spathulata
Parahebe spathulata
Parahebe hookeriana
Parahebe catarractae
Parahebe decora
Parahebe lyallii
Parahebe catarractae
Parahebe canescens
Parahebe linifolia
Parahebe brevistylis
Parahebe vandewateri
Parahebe cheesemanii
Chionohebe densifolia
Chionohebe densifolia
Parahebe trifida
Parahebe birleyi
Chionohebe thomsonii
Chionohebe pulvinaris
Chionohebe ciliolata
Chionohebe ciliolata
Parahebe planopetiolata
Hebe tetrasticha
Hebe ciliolata
Hebe cheesemanii
Hebe cupressoides

long branches are two potentially significant sources of error, both of which could lead to inaccurate estimates of divergence times. Though crude, the estimates nonetheless provide intriguing comparisons with patterns of ecological diversification and aspects of the geological history of New Zealand.

The geological and climatic history of New Zealand suggests that differentiation of the New Zealand hebes is likely to have occurred in the late Tertiary. Members of the basal grade of New Zealand hebes, in particular the *Leonohebe* clade, and the *Chionohebe* A and B clades (Fig. 3), are all alpine or montane plants, most occurring in areas above the natural tree line (Fig. 7). If the present ecological requirements of these groups are indicative of those of their past (i.e., assuming that each lineage has not independently and recently adapted to alpine habitats, or that each has not seen selective extinction of lowland members), it can be inferred that early differentiation of New Zealand hebes occurred in alpine environments, with colonization of the lowlands being a secondary event. The evidence is that alpine environments have only existed in New Zealand since the Pliocene or latest Miocene, subsequent to the onset of mountain building, in what was previously relatively low-lying land (Flemming, 1979; Ollier, 1986).

Prerequisite in any hypothesis of a late Tertiary origin for the New Zealand hebes is colonization of New Zealand by long-distance dispersal of ancestral form(s). Assuming a minimum number of dispersals or extinctions, the topology of cladograms derived from ITS sequences (Figs. 3, 4) suggests that differentiation of New Zealand hebes followed a single colonization from either Australia or Eurasia. This differentiation was succeeded by secondary dispersal from New Zealand.

As illustrated here and elsewhere (Wagstaff & Garnock-Jones, 1998, 2000) the morphology and ITS sequences (Fig. 3) of extant species with transoceanic distributions provide evidence of the capacity of New Zealand hebes for long-distance dispersal. Such transoceanic distributions are seen in four species, all of which are included in our ITS study group, and all of which are nested within the well-supported clade of New Zealand hebes. Of these species, *Hebe elliptica* and *H. salicifolia* naturally occur both in South America and southern New Zealand, whereas *Chionohebe ciliolata* and *C. densifolia* occur both in the South Island of New Zealand and southeastern Australia. Within each of these four species, populations separated by ocean gaps show no apparent morphological differentiation and only limited sequence divergence (Fig. 4). This suggests that the transoceanic disjunctions in the distributions of these species are relatively recent phenomena, and given that these species and all of their closest relatives occur within New Zealand, that these disjunctions are products of long-distance dispersal of propagules from New Zealand.

Godley (1967) suggested oceanic birds as likely vectors for the dispersal of seeds of *H. elliptica* (Fig. 5X) and *H. salicifolia* from New Zealand to South America. Trans-Tasman dispersal of the two alpine *Chionohebe* species from New Zealand to Australia is less intuitively explained owing to the sexual dimorphism of one species (Delph, 1988, 1990), and their splash cup method of seed dispersal (Garnock-Jones, 1993a). The implied direction of dispersal from New Zealand to Australia is also against the prevailing westerly winds but, as noted by Wardle (1978), weather conditions sometimes occur in which the usual direction of winds across the Tasman Sea is reversed. The occurrence of two independent dispersals of *Chionohebe* from New Zealand to Australia may seem unlikely, but the alternative explanations are either an extended period of stasis in both morphology and ITS sequences (assuming distributions produced by fragmentation of Gondwana), or widespread extinction in Australia (assuming dispersal in the opposite direction).

Apart from the dispersal prerequisite to explain transoceanic species distributions, another six dispersal events from the main islands of New Zealand are required to explain the current distribution of *Hebe* (Fig. 6). Most of the postulated dispersals are to New Zealand's outlying islands, including one to the Pleistocene-age (Sykes, 1977) Kermadec Islands (where *Hebe breviracemosa* is endemic), and three to islands of the New Zealand subantarctic (where *H. elliptica* and *H. odora* have populations disjunct from those on the main islands of New Zealand, and *H. benthamii* is endemic). One dispersal to the Chatham Islands has been postulated on morphological grounds (Moore in Allan, 1961; Garnock-Jones, 1976a; Wagstaff & Garnock-Jones, 1998). This is partially supported here by analysis of ITS sequences (Fig. 4), which places two of the endemic species, *H. chathamica* and *H. dieffenbachii*, as sister taxa, and the third, *H. barkeri*, in the polytomy that includes the branch uniting the other two. A final dispersal, probably from the Chatham Islands (Garnock-Jones, 1976a, 1993a), is also postulated to account for the distribution of *H. rapensis* (not included in our analysis), which is endemic on Rapa Island in French Polynesia.

The presence of *Parahebe* in New Guinea is difficult to explain. Here, as in the analysis of Wagstaff and Garnock-Jones (2000), ITS sequence data for

only one New Guinean species of *Parahebe* were included. That species, *P. vanderwateri*, is nested within the New Zealand hebes (Fig. 3) with 99% jackknife support. The most parsimonious interpretation of the present data (assuming a minimum number of dispersals or extinctions) is long-distance dispersal from New Zealand to New Guinea, as proposed by Wagstaff and Garnock-Jones (2000). Further sequence data for New Guinean *Parahebe* (of which 12 species are described) and *Detzneria* (monotypic and endemic) might provide a clearer picture of relationships between taxa from the two areas.

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Appendix 1. Voucher information and GenBank accession numbers for the species of Scrophulariaceae included in our study. Herbarium abbreviations, in parentheses, follow *Index Herbariorum* (Holmgren et al., 1990). Specimens in the CHR herbarium receive a unique accession number (see fourth column) with complete collection information retrievable from this.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	*rbc*L
Amphianthus pusillus Torr.	*C. W. dePamphilis 90.33* (PAC)			Olmstead et al. (2000)		AF123673
Angelonia pubescens Benth.	*C. W. dePamphilis 94.03* (PAC)			Olmstead et al. (2000)		AF123672
Antirrhinum majus L.	*C. W. dePamphilis 90.204* ex hort., University of Michigan (PSU)			Olmstead et al. (1992)		L11688
Bacopa caroliniana B. L. Rob.	*C. W. dePamphilis 90.137* (PAC)			Olmstead et al. (2000)		AF123670
Callitriche heterophylla Pursh emend. Darby	*Philbrick 2152* (CONN)			Olmstead et al. (1992)		L11681
Chelone obliqua L.	*C. W. dePamphilis SS15* (*C. W. Morden 853*) ex hort., Indiana University (PSU)			Olmstead et al. (2000)		AF026824
Chionohebe ciliolata (Hook. f.) B. G. Briggs & Ehrend.	AUSTRALIA. Tasmania, Ben Lomond, Hamilton Crags, *M. J. A. Simpson 8200*		CHR 308581	Wagstaff & Garnock-Jones (2000)	AF229037	
Chionohebe ciliolata (Hook. f.) B. G. Briggs & Ehrend.	NEW ZEALAND. Westland, Wilberg Range, *P. Wardle, R. Buxton, K. Ford*, 27 Apr. 93		CHR 499838	Wagstaff & Garnock-Jones (2000)	AF229037	
Chionohebe densifolia (F. Muell.) B. G. Briggs & Ehrend.	AUSTRALIA. Northcote Pass, Main Range, Kosciusco Alpine Area at 2100 m. *T. Armstrong*		CHR 536185	this paper	AY034849	
Chionohebe densifolia (F. Muell.) B. G. Briggs & Ehrend.	NEW ZEALAND. 'Hokonui Alpines,' *P. Heenan* 9.3.90	G19236	CHR 512454	Wagstaff & Garnock-Jones (1998)	AF037375	AY034007
Chionohebe pulvinaris (Hook. f.) B. G. Briggs & Ehrend.	NEW ZEALAND. Nelson, Mt. Arthur, summit trig point, *W. R. Sykes 551/93*	551/93	CHR 496926	Wagstaff & Garnock-Jones (2000)	AF229038	
Chionohebe thomsonii (Buchanan) B. G. Briggs & Ehrend.	NEW ZEALAND. Fog Peak, *P. Heenan, P. J. Garnock-Jones* 8.12.89	G18586	CHR 512485	Wagstaff & Garnock-Jones (2000)	AF229039	
Collinsia grandiflora Lindl.				Olmstead et al. (2000)		AF026825
Derwentia derwentiana (Andrews) B. G. Briggs & Ehrend.	AUSTRALIA. Tasmania, *A. T. Dobson 77180*	G11573	CHR 512469	Wagstaff & Garnock-Jones (1998)	AF037381	
Derwentia nivea (Lindl.) B. G. Briggs & Ehrend.	AUSTRALIA. Cultivated Landcare Research Experimental Garden *Wagstaff 94.105*	G19629	CHR 512486	Wagstaff & Garnock-Jones (1998)	AF037382	AY034010
Derwentia perfoliata (R. Br.) Raf.	AUSTRALIA. Cultivated Landcare Research Experimental Garden *Wagstaff 94.40*		CHR 512493	Wagstaff & Garnock-Jones (2000)	AF229040	—

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession ITS	GenBank accession *rbc*L
Digitalis purpurea L.	unknown			Olmstead et al. (1993)		L01902
Globularia cordifolia L.	*L. Hufford*, no voucher			Olmstead et al. (2000)		AF124558
Gratiola pilosa Michx.	*C. W. dePamphilis 90.34*			Olmstead et al. (2000)		AF026827
Hebe albicans (Petrie) Cockayne	NEW ZEALAND. Northwest Nelson, Boulder Lake, *D. Rooney* 5.2.88	G17134	CHR 512448	Wagstaff & Garnock-Jones (1998)	AF037373	
Hebe annulata (Petrie) Cockayne & Allan	NEW ZEALAND. Southland, Wye River near Lake Wakatipu, *P. Wardle, N. Simpson*, Dec. 1994	366/94	CHR 512497	Wagstaff & Wardle (1999)	AF069464	
Hebe armstrongii (J. B. Armstr.) Cockayne & Allan	NEW ZEALAND. Canterbury, Enys Reserve, *B. Molloy* 20.385	G16006	CHR 512483	Wagstaff & Wardle (1999)	AF069463	
Hebe barkeri (Cockayne) Cockayne	NEW ZEALAND. Chatham Island, *D. R. Given 121-85*	G16061	CHR 512496	Wagstaff & Garnock-Jones (1998)	AF037374	
Hebe benthamii (Hook. f.) Cockayne & Allan	NEW ZEALAND. Campbell Island, Beeman Hill, *B. D. Rance* 17 Nov. 1990		CHR 468050	this paper; Wagstaff & Garnock-Jones (2000)	AF229041	AY034013
Hebe chathamica (Buchanan) Cockayne & Allan	NEW ZEALAND. Chatham Islands, Kaingaroa, *D. R. Given 12830, P. A. Williams*	G14675	CHR 512434	Wagstaff & Garnock-Jones (1998)	AF037387	
Hebe cheesemanii (Buchanan) Cockayne & Allan	NEW ZEALAND. Marlborough, George Stream, *P. Heenan, P. J. Garnock-Jones 1999*	49/91	CHR 512472	Wagstaff & Garnock-Jones (1998)	AF037377	AY034008
Hebe ciliolata (Hook. f) Cockayne & Allan	NEW ZEALAND. Nelson, Havelock Valley, *D. Rooney*, 15.4.99	292/91	CHR 512474	this paper	AY034851	—
Hebe cockayneana (Cheeseman) Cockayne & Allan	NEW ZEALAND. Southland, Gertrude Valley, *P. J. Garnock-Jones 1883*	G17527B	CHR 512443	Wagstaff & Garnock-Jones (1998)	AF037399	
Hebe corriganii Carse	NEW ZEALAND. South Auckland, McLarens Falls, *P. J. Garnock-Jones, B. D. Clarkson 1984*	G1/09B	CHR 512458	Wagstaff & Garnock-Jones (1998)	AF037384	
Hebe cupressoides (Hook. f.) Cockayne & Allan	NEW ZEALAND. Canterbury, Rakaia Gorge, *R. Buxton*, 15 Dec. 1989	G18637	CHR 512449	Wagstaff & Garnock-Jones (1998)	AF037378	AY034014
Hebe dieffenbachii (Benth.) Cockayne & Allan	NEW ZEALAND. Chatham Islands, Kaingaroa, *D. R. Given 14015*	G15933	CHR 512462	this paper	AY034852	—
Hebe elliptica (G. Forst.) Pennell	ARGENTINA. Falkland Island, Carcass Id, *U. McHardy*		WELTU 16897	Wagstaff & Garnock-Jones (1998)	AF037392	AY034011

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession ITS	GenBank accession *rbc*L
Hebe elliptica (G. Forst.) Pennell	NEW ZEALAND. Cultivated Landcare Research experimental garden, originally from Mt. Peel Nursery, *P. Heenan. 12.9.89*		CHR 512484	Wagstaff & Garnock-Jones (1998)	AF037393	—
Hebe epacridea (Hook. f.) Cockayne & Allan	NEW ZEALAND. Canterbury, Mt. Terako, *S. J. Wagstaff 95.01*		CHR 512479	Wagstaff & Garnock-Jones (1998)	AF037389	
Hebe formosa (R. Br.) Cockayne	AUSTRALIA. Botanic Gardens, Canberra 8704379	186/94	CHR 512490	Wagstaff & Garnock-Jones (1998)	AF037383	AY034015
Hebe hectorii (Hook. f.) Cockayne & Allan subsp. *hectorii*	NEW ZEALAND. Southland, Takitimu Range, *P. J. Garnock-Jones 1925*	G18884	CHR 512450	Wagstaff & Wardle (1999)	AF069460	
Hebe hectorii subsp. *subsimilis* (Colenso) Wagstaff & Wardle	NEW ZEALAND. Hawkes Bay, Ngamoko Range (spur of Ruahine Range), *A. P. Druce* Apr. 1978		CHR 323681	Wagstaff & Garnock-Jones (1998)	AF037390	
Hebe lycopodioides (Hook. f.) Cockayne & Allan subsp. *lycopodioides*	NEW ZEALAND. Canterbury, Mt. Terako, *S. J. Wagstaff 95.03*		CHR 512480	Wagstaff & Wardle (1999)	AF069456	
Hebe macrantha (Hook. f.) Cockayne & Allan	NEW ZEALAND. Nelson, Matiri Plateau *D. Glenny, S. J. Wagstaff 95.09*		CHR 512468	this paper	AY034853	—
Hebe macrantha (Hook. f.) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research experimental garden, originally from Christchurch Botanic Garden, *P. Heenan* 17.11.89	G18370	CHR 512444	Wagstaff & Garnock-Jones (1998)	AF037391	AY034016
Hebe odora (Hook. f.) Cockayne	NEW ZEALAND. Mt. Peel Nursery, *P. J. Garnock-Jones* 4 Dec. 1990	G17812	CHR 512441	Wagstaff & Garnock-Jones (1998)	AF037388	AF034017
Hebe parviflora (Vahl) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, originally from Mt. Peel Nursery, *P. Heenan* 12.9.89	G17820	CHR 512447	this paper	AY034854	—
Hebe pauciramosa (Cockayne & Allan) L. B. Moore	NEW ZEALAND. Canterbury, Mt. Somers, *D. Rooney* 5.5.88	G17158	CHR 512461	Wagstaff & Wardle (1999)	AF069466	
Hebe petriei (Buchanan) Cockayne & Allan	NEW ZEALAND. Southland, Eyre Creek, *P. J. Garnock-Jones 1965*	G18708B	CHR 512498	Wagstaff & Garnock-Jones (2000)	AF229042	
Hebe pimeleoides (Hook. f.) Cockayne & Allan	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, ex. *J. Cartman* 19.9.89	G17906		this paper	AY034855	—

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	*rbc*L
Hebe propinqua (Cheeseman) Cockayne & Allan	NEW ZEALAND. Southland, South Mavora Lake, *P. Wardle* 30.3.95	107/93B	CHR 512478	Wagstaff & Wardle (1999)	AF069458	
Hebe ramosissima G. Simpson & J. S. Thomson	NEW ZEALAND. Marlborough, Mt. Tapuaenuku, *J. Cartman* 9.1.90	G18659	CHR 512628	this paper	AY034856	
Hebe salicifolia (G. Forst.) Pennell	CHILE. San Rafael, *R. Buxton 1992*		WELTU 16898	Wagstaff & Garnock-Jones (1998)	AF037386	AY034018
Hebe salicifolia (G. Forst.) Pennell	NEW ZEALAND. Nelson, Matiri Plateau, *S. J. Wagstaff 95.10*		CHR 512466	Wagstaff & Garnock-Jones (1998)	AF037385	
Hebe salicornioides (Hook. f) Cockayne & Allan	NEW ZEALAND. Canterbury, Jacks Pass, Hanmer, *J. B. Hair* 26.10.66	G6602	CHR 512475	Wagstaff & Wardle (1999)	AF069465	AY034019
Hebe speciosa (A. Cunn.) Cockayne & Allan	NEW ZEALAND. North Auckland, Maunganui Bluff, *D. R. Given, J. Bartlett 11571*	G12051	CHR 512457	this paper	AY034864 AY034865	
Hebe tetrasticha (Hook. f) Cockayne & Allan	NEW ZEALAND. Canterbury, Mt. Cheeseman, *A. P. Druce* 20.10.89	G18476	CHR 512451	this paper	AY034866 AY034867	
Hebe townsonii (Cheeseman) Cockayne & Allan	NEW ZEALAND. Northwest Nelson, Coastal, A. W. Purdie 29.1.88.	G17111	CHR 152489	this paper	AY034857	
Hebe vernicosa (Hook. f.) Cockayne & Allan	NEW ZEALAND. Nelson, Maungatapu Summit, *P. J. Garnock-Jones 1888*	G17557E	CHR 465635	this paper	AY034858	
Heliohebe hulkeana (F. Muell.) Garn.-Jones	NEW ZEALAND. Marlborough, Ure River, *D. Given* 31.1.1966	G17113	CHR 512460	Wagstaff & Garnock-Jones (1998)	AF037379	
Heliohebe lavaudiana (Raoul) Garn.-Jones	NEW ZEALAND. Canterbury, Banks Peninsula, Summit Road, *B. Molloy* 8.9.82	G14806	CHR 512487	Wagstaff & Garnock-Jones (2000)	AF229043	
Heliohebe raoulii (Hook. f.) Garn.-Jones	NEW ZEALAND. Marlborough, Mt. Fyffe, *L. Decourtye* 22.2.86	G16285	CHR 512459	Wagstaff & Garnock-Jones (1998)	AF037380	AY034009
Hippuris vulgaris L.	*Olmstead & Reeves 92–127*			Olmstead & Reeves (1995)		L36443
Parahebe birleyi (N. E. Br.) W. R. B. Oliv.	NEW ZEALAND. Southland, Takitimu Range, above tarn in cirque E of Tower Peak, 1340 m, *P. J. Garnock-Jones 2039, W. M. Malcolm*		CHR 470104	Wagstaff & Garnock-Jones (2000)	AF229044	
Parahebe brevistylis (Garn.-Jones) Heads	NEW ZEALAND. Southland Eyre Mountain, Upper Eyre Creek, *P. J. Garnock-Jones 1910*	G18892	CHR 512452	Wagstaff & Garnock-Jones (2000)	AF229045	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession ITS	GenBank accession *rbc*L
Parahebe canescens W. R. B. Oliv.	NEW ZEALAND. Canterbury, S end of Lake Lyndon, *P. J. Garnock-Jones*, Aug. 1990	264/90	CHR 512446	Wagstaff & Garnock-Jones (1998)	AF037394	
Parahebe catarractae subsp. *martinii* Garn.-Jones	NEW ZEALAND. Marlborough, Waima River, *P. A. William* 15.4.1976s	G11359	CHR 512456	Wagstaff & Garnock-Jones (1998)	AF037396	AY034020
Parahebe catarractae (G. Forst.) W. R B. Oliv. subsp. *catarractae*	NEW ZEALAND. Otago, Manapouri Wilmot Pass Rd., *P. J. Garnock-Jones 2403*			this paper	AY034859	
Parahebe cheesemanii (Benth.) W. R. B. Oliv.	NEW ZEALAND. Nelson, St. Arnaud Range, basin W of Rainbow Snowfield, *B. D. Rance, L. Lewington* 2 Apr. 1994		CHR 509212	Wagstaff & Garnock-Jones (2000)	AF229046	
Parahebe decora Ashwin	NEW ZEALAND. Nelson, Matiri Plateau, *D. Glenny, S. J. Wagstaff 95.08*		CHR 512467	Wagstaff & Garnock-Jones (2000)	A229047	
Parahebe hookeriana (Walp.) W. R. B. Oliv.	NEW ZEALAND. Wellington, Mt. Ruapehu, *P. J. Garnock-Jones 2416*			this paper	AY034860	
Parahebe linifolia (Hook. f.) W. R. B. Oliv.	NEW ZEALAND. Canterbury, Havelock Valley, Carney's Creek Hut, *B. P. J. Molloy, A. P. Druce* 22 Feb. 1991	182/91	CHR 470347	Wagstaff & Garnock-Jones (2000)	AF229047	
Parahebe lithophila B. G. Briggs & Ehrend.	AUSTRALIA. New South Wales, 1 km on track below McMahons Lookout, ca. 5 km S of Wentworth Falls, Blue Mountains Natl. Park, *B. G. Briggs, B. Wiecek, L. Johnson* 2.5.92		CHR 454303	Wagstaff & Garnock-Jones (2000)	AF229048	
Parahebe lyallii (Hook f.) W. R. B. Oliv.	NEW ZEALAND. North Canterbury, Mt. Percival, *A. W. Purdie* 11.5.89	G17594	CHR 512440	Wagstaff & Garnock-Jones (1998)	AF037395	
Parahebe planopetiolata (G. Simpson & J. S. Thomson) W. R. B. Oliv.	NEW ZEALAND. Southland, Kingston, Mt. Dick, Lake Wakatipu, *N. Simpson* 15.5.95	147/95	CHR 512626	Wagstaff & Garnock-Jones (2000)	AF229050	
Parahebe spathulata (Benth.) W. R. B. Oliv.	NEW ZEALAND. Cultivated Victoria University, *P. J. Garnock-Jones 2404*			this paper	AY034861	
Parahebe spathulata (Benth.) W. R. B. Oliv.	NEW ZEALAND. Volcanic Plateau, Mt. Ruapehu, Turoa Skifield, beside buildings at top of road, 1600 m, *P. J. Garnock-Jones* 2263		WELTU 16860	Wagstaff & Garnock-Jones (2000)	AF229051	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession	
					ITS	*rbc*L
Parahebe trifida W. R. B. Oliv.	NEW ZEALAND. Southland, Garvie Mts. Mt. Tennyson, E slope near summit, 1460 m, *P. J. Garnock-Jones 2161*		CHR 512442	Wagstaff & Garnock-Jones (1998)	AF037376	
Parahebe vandewateri (Pennell) P. Royen	NEW GUINEA. Neren Vally, M3, 4180 m, near clear-colored lake, *R. Buxton*, 12 Sep. 1998		CHR 530002	Wagstaff & Garnock-Jones (2000)	AF229052	AY034023
Plantago lanceolata L.	*Olmstead s.n.*			Olmstead & Reeves (1995)		L36454
Pseudolysimachion spicatum Opiz	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313022	
Veronica anagallis-aquatica L.	NEW ZEALAND. Canterbury, Harts Creek, *S. J. Wagstaff 94.09*		CHR 512465	Wagstaff & Garnock-Jones (1998)	AF037397	AY034021
Veronica arguta R. Br.	AUSTRALIA. Cultivated Landcare Research Experimental Garden, originally from Botanic Gardens, Canberra, 8704379	186/94	CHR 512625	this paper	AY034862	AY034025
Veronica austriaca L.	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313000	
Veronica bellidioides L.	AUSTRIA. Karnten: Nockberge Hoher Falkert, *J. P. Grube*, MWC 7416 (K)	KEW 1996-761		Albach & Chase (2001)	AF313010	
Veronica calycina R. Br.	AUSTRALIA. Cultivated Landcare Research Experimental Garden, originally from Botanic Gardens, Canberra 8602018	187/94	CHR 512627	this paper	AY034863	
Veronica chamaedrys L.	NORWAY. Horsland: Os, Hattvik, MWC 7419 (K)	KEW 1970-1438		Albach & Chase (2001)	AF313003	
Veronica fruticulosa L.	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313004	
Veronica glandulosa Hochst.	KENYA. *Fischer 713/98*	Bot. Garden Bonn		Albach & Chase (2001)	AF313008	
Veronica glauca Sibth. & Sm.	GREECE. RBG Kew, MWC 8922 (K)	KEW 1973-14554		Albach & Chase (2001)	AF313006	
Veronica macrostachya Vahl	Unknown, RBG Kew, MWC 7417 (K)	KEW 1969-50547		Albach & Chase (2001)	AF312999	
Veronica officinalis L.	ITALY. Reg. Calabria, Prov. Coseniza, *S. P. Brooks 23 July 1984*		CHR 423831	this paper		AY034024
Veronica officinalis L.	GREAT BRITAIN. Farthing Downs, MWC 7385 (K)	KEW 1978-1342		Albach & Chase (2001)	AF313024	
Veronica oltensis Woron.	TURKEY. NYBG, *L. Struwe 1405* (WU)	NYBG		Albach & Chase (2001)	AF312995	

Appendix 1. Continued.

Species	Original locality/source	Garden accession	Herbarium accession	Literature citation	GenBank accession ITS	GenBank accession *rbc*L
Veronica persica Poir.	NEW ZEALAND. Canterbury, Lincoln, Agricultural and Science Research Centre, adventive, *S. J. Wagstaff 94.04*		CHR 512455	this paper	AY036878	AY034023
Veronica persica Poir.	*Olmstead 92–144*			Olmstead & Reeves (1995)		L36453
Veronica saturejoides Vis.	Unknown, NYBG, *L. Struwe 1408* (WU)			Albach & Chase (2001)	AF313005	
Veronica serpyllifolia L.	NEW ZEALAND. Canterbury, Groynes Nature Reserve, adventive along lake shore, *S. J. Wagstaff 95.55*		CHR 518833	this paper	AY036879	
Veronica urticifolia Jacq.	Unknown, Bot. Garden Bonn		s.n., BONN	Albach & Chase (2001)	AF313011	
Veronicastrum sibiricum (L.) Pennell	NEW ZEALAND. Cultivated Landcare Research Experimental Garden, *S. J. Wagstaff, P. J. Garnock-Jones 94.09*		CHR 512445	Wagstaff & Garnock-Jones (1998)	AF307398	AY034012
Wulfenia carinthiaca Jacq.	AUSTRIA. Karnten, Gartnerkofel	Bot. Garden Bonn	s.n., BONN	Albach & Chase (2001)	AF313025	

PHYLOGENETIC RECONSTRUCTION OF THE NEOTROPICAL FAMILY QUIINACEAE (MALPIGHIALES) BASED ON MORPHOLOGY WITH REMARKS ON THE EVOLUTION OF AN ANDRODIOECIOUS SEX DISTRIBUTION[1]

Julio V. Schneider,[2] Ulf Swenson,[3] and Georg Zizka[2]

Abstract

Based on morphology, a cladistic analysis of the Neotropical family Quiinaceae (Malpighiales) was performed to generate a hypothesis of the phylogenetic relationships within the family. The monotypic Medusagynaceae and four species of Ochnaceae were used as outgroup. Using equal weights, the Quiinaceae find strong jackknife support and all genera, apart from *Lacunaria*, are monophyletic. *Lacunaria* receives support only after successive weighting. The aberrant species *Lacunaria oppositifolia* and *Quiina pteridophylla* are positioned within their respective genera, although separation of the former as monotypic cannot be discarded with certainty. Proposed close relationship of the two species is rejected. *Froesia* is the morphologically most distinguished genus and sister to all other taxa of the family. *Touroulia amazonica*, once suggested to be recognized at the generic level, forms a small but closely related clade with *T. guianensis*. *Quiina* is the most diverse and derived genus with highly unresolved relationships and numerous polymorphic characters. A reduction toward smaller inflorescences and flowers, fewer stamens, and fewer carpels can be hypothesized. Concerning the evolution of sex distribution, androdioecy was fixed early in a common ancestor of *Lacunaria*, *Quiina*, and *Touroulia*, and subsequently dioecy evolved in *Lacunaria*.

Key words: Androdioecy, *Froesia*, *Lacunaria*, morphology, phylogenetic analysis, *Quiina*, Quiinaceae, *Touroulia*.

The Quiinaceae are a Neotropical dicotyledonous family of 51 species, including several taxa not yet described. It presently comprises *Froesia* Pires (5 species), *Lacunaria* Ducke (10 species), *Quiina* Aubl. (34 species), and *Touroulia* Aubl. (2 species). The Quiinaceae occur principally in primary lowland rainforests, with a few species found in premontane and cloud forests, reaching an elevation of about 1500 m a.s.l. The family is distributed from Belize and Jamaica to southern Brazil and Bolivia with a center of diversity in the Amazon lowland forests (Fig. 1), and it comprises shrubs or medium-sized trees. While the systematic position of the family within the Malpighiales seems to be comparatively clear, recent studies have proposed embedding Quiinaceae in Ochnaceae on the basis of a single gene, the *rbc*L (Chase et al., 2000; Savolainen et al., 2000). However, this systematic amalgamation may not find support if additional molecular markers and/or morphology are considered (e.g., Soltis et al., 2000; Jansen et al., 2001). The infrafamilial systematics, despite the important contributions of Pires (1948, 1950, 1953, 1960), still raises many questions due to our incomplete knowledge of the family, an issue we wish to address in this paper.

Circumscription and mutual relationships of the genera of Quiinaceae are issues not hitherto inves-

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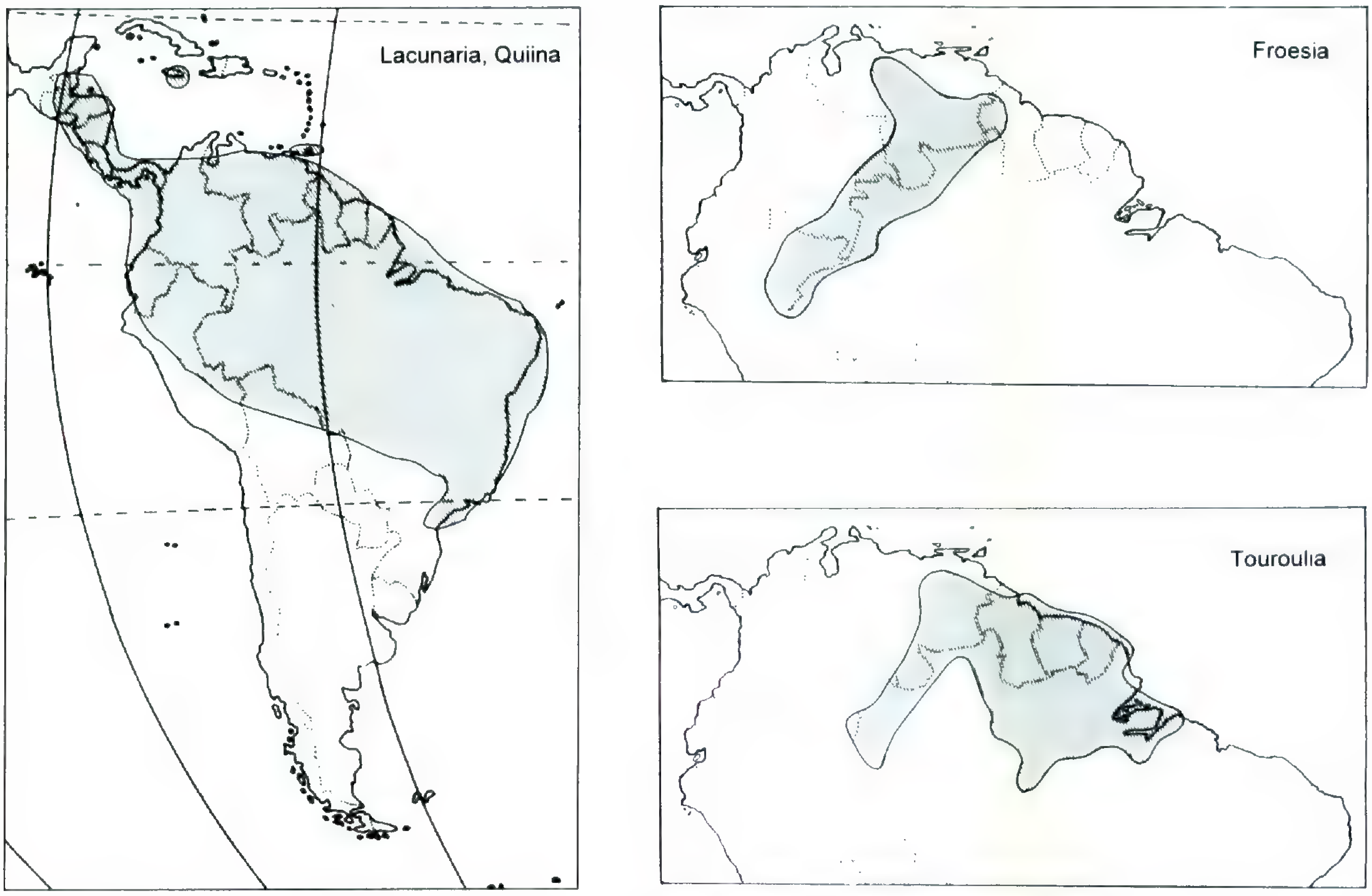

Figure 1. Distribution of the neotropical family Quiinaceae: *Lacunaria* and *Quiina*, circumscribing 10 and 35 species, respectively; *Froesia* with 5 species; and *Touroulia*.

tigated in a cladistic framework. Based on anatomical data, *Froesia* was postulated to have a somewhat isolated position in the family (Gottwald & Parameswaran, 1967). While *Froesia* forms a homogeneous, easily identified group, the two *Touroulia* species differ from each other, especially in anatomical characters, and the question arises whether they form a monophyletic group. Delimitation of species and generic boundaries are especially difficult to discern in *Quiina* and *Lacunaria*. The latter is comprised of a "core group" of similar species plus a few species more or less aberrant. The systematic position of *Lacunaria oppositifolia* Pires is uncertain, and generic rank for this taxon has been proposed (Pires, in sched.). Similarly, generic rank was proposed for *Touroulia amazonica* Pires & A. S. Foster (Pires, in sched.). *Quiina pteridophylla* (Radlk.) Pires is another puzzling species, being intermediate between *Quiina* and *Lacunaria* in several morphological characters.

In flowering plants, sex distribution is an important character for understanding the evolution of androdioecy and dioecy. Evolutionary hypotheses concerning mating systems have been postulated and reviewed in the light of population genetics (sexual selection, sex allocation theory) (Ross, 1978, 1982; Bawa, 1980; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Pannell, 1997) or phylogenetic constraints (Swensen et al., 1998). As evidenced by the existence of androdioecy (and dioecy) in different, rather divergent major taxa, it most probably originated independently and several times from hermaphroditism (Swensen et al., 1998). Careful examination shows that most of these species are only morphologically androdioecious, but functionally dioecious because of inviable pollen or indehiscent anthers. Functional androdioecy is very rare in seed plants. According to Swensen et al. (1998) it is known only from four species: *Datisca glomerata* (C. Presl) Baill. (Datiscaceae), *Mercurialis annua* L. (Euphorbiaceae), *Saxifraga cernua* A. Gray (Saxifragaceae), and *Phillyrea angustifolia* L. (Oleaceae). An additional species, *Schizopepon bryoniifolius* Maxim. (Cucurbitaceae), was reported by Akimoto et al. (1999). In Quiinaceae, *Froesia* has perfect flowers, *Touroulia* and *Quiina* are androdioecious, and *Lacunaria* is dioecious. The morphologically androdioecious genus *Quiina* is probably functionally dioecious too, producing inaperturate pollen in morphologically hermaphroditic plants (Pires, cited after Kubitzki, 1995 pers. comm.; Schneider, 1998).

With respect to the monophyly of Quiinaceae, all species share a characteristic combination of anatomical characters of wood and bark (Gottwald &

Table 1. Characters and character states for the Quiinaceae and the outgroups *Elvasia*, *Ouratea* (Ochnaceae), and *Medusagyne* (Medusagynaceae).

1. Plants not caulirosulate (0); caulirosulate (1).
2. Terminal internodes terete (0); laterally conspicuously compressed (1).
3. Leaves alternate (0); opposite (1); verticillate (2).
4. Adult leaves simple (0); compound (1).
5. Leaf rachis absent (0); not alate (1); alate (2).
6. Leaf blade or leaflet ovate (0); elliptic (1); obovate (2).
7. Leaf blade or leaflet glabrous or principal vein pubescent (0); principal vein and leaf surface along the veins pubescent (1); abaxial surface pubescent (2).
8. Leaf or leaflet apex acuminate to acute (0); obtuse (1); retuse (2).
9. Leaf or leaflet margin revolute (0); flat (1).
10. Leaf or leaflet margin entire (0); minutely serrulate (1); serrate (2).
11. Leaf or leaflet vein apices not protruding or reaching the margin (0); conspicuously protruding from lamina margin into teeth (1).
12. Number of teeth less than secondary veins (0); more teeth than secondary veins (1); teeth equal in number to secondary veins (2); teeth absent (3).
13. Venation craspedodromous (0); camptodromous (1).
14. Prominence of leaf venation: abaxially more prominent (0); abaxially and adaxially ± equally prominent (1); adaxially more prominent (2).
15. Intersecondary veins not developed (0); conspicuously developed (1); present but not conspicuously developed (2).
16. Tertiary veins scalariform (0); parallel (1); plumose-reticulate (2); reticulate (3).
17. Stomata paracytic (0); anomocytic (1).
18. Stomata positioned on a flat abaxial surface (0); in small depressions (1).
19. Petioles canaliculate (0); terete (1).
20. Petiole base not conspicuously broadened (0); pulvinoid broadened, not distinguishable from upper part (1); pulvinoid broadened, distinguishable from upper part (2).
21. Stipules not interpetiolar (due to alternate phyllotaxis) (0); interpetiolar (1); absent (2).
22. Stipules free (0); partly fused with deep, subulate lobes (1); completely fused (2).
23. Stipules persistent (0); caducous (1).
24. Stipules glabrous (0); pubescent (1).
25. Stipules sessile (0); stipitate (1).
26. Stipule margins entire (0); serrulate (1).
27. Stipule lobe(s) cuspidate (0); acuminate to acute (1); obtuse (2).
28. Plants hermaphroditic (0); andromonoecious (1); androdioecious (2); dioecious (3).
29. Inflorescence terminal (0); axillary (1).
30. Inflorescence glabrous (0); inconspicuously pubescent with trichomes mostly <0.2 mm long (1); conspicuously pubescent (velvety, tomentose) with trichomes mostly >0.3 mm long (2).
31. Inflorescence branched with one main axis (0); branched with several axes, fasciculate (1); unbranched (2).
32. Staminate flowers absent (0); in groups of 1 to 3 on terminal branches (1); in groups of 4 to 12 on terminal branches (2).
33. Pedicel in upper part slightly widened to cylindrical (0); obconical (1).
34. Pedicel articulation between base and 1/3 of the length (0); clearly more than 1/3 of length (1).
35. Pedicel (upper part) glabrous (0); pubescent (1).
36. Sepals 2 or 3 (0); 4 (1); 5 to 8 (2).
37. Sepal texture membranous (0); coriaceous (1).
38. Sepals glabrous (0); margin pubescent (1); margin and abaxial surface pubescent (2).
39. Sepals monomorphic, size equal (0); heteromorphic, outer smaller than inner (1).
40. Petal aestivation imbricate (0); contorted (1).
41. Petal margin (best observed in bud) glabrous (0); pubescent (1).
42. Petals obovate (0); elliptical (1).
43. Petal apices rounded (0); notched (1).
44. Functional stamens in hermaphroditic or staminate flowers 10 to 25 (0); 30 to 80 (1); >100 (2).
45. Filaments basally free from petals (0); adnate (1).
46. Anthers (in outline) elongate, linear-oblong (0); narrowly elliptic (1); ± round (2).
47. Anthers opening by apical pores (0); longitudinal slits (1).
48. Gynoecium syncarpous (0); apocarpous (1).
49. Carpels 2 (0); 3 (1); 4 to 8 (2); 10 to 14 (3); >16 (4).

Table 1. Continued.

50. Ovules per locule 1 (0); 2 (to 4) (1).
51. Some ovules abort (0); all ovules develop to seeds (1).
52. Fruit a capsule (0); berry (1); follicle (2); schizocarp of mericarps (3); dry, indehiscent (4).
53. Fruit apex rounded, centrally ± concave (0); conical, ± acute (1).
54. Fruits not spotted (0); with yellowish spots (1).
55. Fruit pericarp in transverse section without lacunae (0); inconspicuous lacunae (1); conspicuous lacunae (2).
56. Fruits glabrous (0); pubescent (1).
57. Exocarp of mature fruits smooth (0); longitudinally furrowed by underlying lacunae (1); fruit appearing conspicuously ribbed (2).
58. Seeds glabrous (0); pubescent (1).
59. Seeds longer than wide, ellipsoid (0); as long as wide, globose (1).
60. Crystalliferous cells abundant, in long rows along the veins (0); not abundant, sometimes in groups near the veins (1).
61. Crystalliferous cells without special thickening of cell wall (0); always present, with u-shaped thickening (1).

Parameswaran, 1967). An unusual craspedodromous leaf venation with very closely spaced tertiary veins is found in *Touroulia*, *Froesia*, and *Lacunaria* (a slightly different pattern is observed in *Quiina*), a set of characters also regarded as unique to the family (Foster, 1950a, b, 1951; Roth, 1996; Zizka & Schneider, 1999). *Froesia* and *Touroulia guianensis* Aubl. display a characteristic u-shaped thickening of the cell wall (cristarque cells) (unpublished data). Another common character is the presence of mucilaginous cavities, particularly in petioles (Schofield, 1968), and is frequently observed in all genera.

Quiinaceae have formerly been regarded as part of the order Theales (Cronquist, 1981). More recently, phylogenetic studies based on DNA sequence data (*rbc*L, *atp*B, and 18S) place the family in Malpighiales (Fay et al., 1997; Källersjö et al., 1998; Litt & Chase, 1998; Nandi et al., 1998; Chase, 1996, pers. comm.). This position was accepted in the ordinal classification of the flowering plants recently published by the Angiosperm Phylogeny Group (APG, 1998). These studies suggest that the closest relatives of Quiinaceae are Ochnaceae and/or Medusagynaceae. Despite this affinity, the relationship between each of these families is weak. In the study by Nandi et al. (1998), Quiinaceae are sister to Ochnaceae when based solely on weighted *rbc*L parsimony. When combined with non-molecular data, Quiinaceae shift and lie basal to the sister pair of Ochnaceae and Medusagynaceae. The positioning of Medusagynaceae, Ochnaceae, and Quiinaceae within the Malpighiales was unstable depending on character sets used.

For the forthcoming treatment of Quiinaceae for the *Flora Neotropica* (Schneider & Zizka, in prep.), the present study based on morphology attempts to resolve questions of generic circumscription, including morphological synapomorphies. We also investigate the affinities of the aberrant species *Lacunaria oppositifolia*, *Quiina pteridophylla*, and *Touroulia amazonica*. Finally, we provide a familial interpretation of gynoecium morphology and sex distribution in a phylogenetic perspective.

Data and Methods

Taxa

Ingroup monophyly is necessary for correct rooting of the tree (Nixon & Carpenter, 1993). The outgroup was therefore chosen from the two most closely related families, Ochnaceae and Medusagynaceae (*Medusagyne oppositifolia* Baker). Gottwald and Parameswaran (1967) already pointed out that the most closely related family to Quiinaceae is Ochnaceae, and herein the tribes Elvasieae Engl. and Ourateeae Baill. of the former Exalbuminosae sensu Engler. Hence, two species each of the genera *Elvasia* DC. and *Ouratea* Aubl. were selected. Because information on infrageneric relationships within the outgroup is lacking, the species included in the analysis were selected according to the criteria of (1) their distribution within the geographical range of Quiinaceae, (2) their previous use in cladistic analyses (Amaral, 1991), and (3) the number of specimens available for detailed morphological and anatomical studies.

Within the ingroup, a total of 22 species were included as terminal taxa. Since the principal intention of the study was the resolution of generic relationships within the family, it was considered redundant to include all species. The present selection comprises representatives of all genera and, more importantly, all somewhat aberrant species as well as core representatives from *Lacunaria* and *Quiina*. *Froesia* is, on one hand, a comparatively

homogeneous group; on the other hand, it is the most distinct genus within the family. Thus, three species were chosen and regarded as sufficient because the inclusion of all its species would not change the principal topology of the cladogram. *Quiina* is represented by 12 out of its 34 species, many of which are difficult to diagnose and circumscribe because of remaining taxonomic and nomenclatural problems.

CHARACTERS AND CHARACTER STATES

Characters were extracted from morphological studies undertaken (see Table 1); the final data matrix appears in Table 2. Multistate characters are generally unordered in phylogenetic reconstruction, but if there is reason to believe a character state is intermediate between two other states, such a character may be ordered (Wilkinson, 1992, 1995). In our analysis, only two characters (6 and 8) could be treated as ordered. These refer to leaf outline and leaf apices where an intermediate transition state can be perceived. Unknown character states are coded with a question mark (?) and inapplicable states with a dash (-). Character evolution was traced by using the software MacClade (Maddison & Maddison, 1992).

Autapomorphies can either be included or excluded in phylogenetic reconstruction. Yeates (1992) argued that removal may also remove information from a data matrix, but Bryant (1995) disagreed, saying that they should be removed. Arguments against autapomorphies rest on the fact that they are unique, uninformative, and inflate the consistency index (CI). Phylogenetic reconstruction, however, is much more than consistency indices. This study, for example, aims to reconstruct the major evolutionary lineages within Quiinaceae with approximately a third of the species of *Quiina* sampled. To facilitate future studies using a wider sampling, autapomorphies were therefore included to avoid excluding potential synapomorphies.

Polymorphic characters are abundant in Quiinaceae and can be treated in different ways. For example, they could be coded as missing entries, which then introduce erroneous consistency indices and tree length (Nixon & Davis, 1991). Polymorphic characters could also be included and scored for the observed intraspecific variation, albeit a low phylogenetic signal (Wiens, 1995). Kornet and Turner (1999) recommended that polymorphic characters should be coded as plesiomorphic in favor of the observed intraspecific variation unless the ancestral state is unknown. Assessment of the ancestral state, at least in Quiinaceae, is a critical point and generally lacking. Since we believe that polymorphic characters do provide a phylogenetic signal and resolution, they are scored with the observed states.

Habit. Plants are caulirosulate in *Froesia*, which means that leaves are crowded at the stem or branch apex (char. 1).

Leaves. The presence of compound versus simple leaves (char. 4) is problematic with respect to homology and comparability of character states. For the current analysis the single leaflets of species with compound leaves are regarded as homologous to simple leaves because they are functionally equivalent units (Raunkiaer, 1934). Furthermore, this reflects the equivalent venation pattern of leaflets and simple leaves. Additional support is given by the presence of simple leaves in seedlings of pinnate-leaved *Froesia venezuelensis* Steyerm. & G. S. Bunting and pinnatifid leaves in seedlings of simple-leaved *Quiina pteridophylla*. In *Quiina* and *Lacunaria* the leaf margin (char. 10) can be inconspicuously serrulate, only seen with a strong lens (magnification > 20×). In this case minute incisions or papillae are seen. The pattern of leaf venation is a peculiar and particularly important character in Quiinaceae (Foster, 1950a, b, 1951; Roth, 1996). All Quiinaceae exhibit a craspedodromous type (char. 13; classification following Hickey, 1973, 1979). The presence of conspicuous intersecondary veins (char. 15) discriminates *Quiina* and is regarded as a synapomorphy for the genus. Intersecondary veins have a diameter intermediate between secondary and tertiary veins; they originate from the primary vein and do not reach the leaf margins. In camptodromous *Medusagyne* it is hard to judge the intermediate veins as distinct intersecondaries. For the analysis they are considered as inconspicuously developed intersecondary veins. The tertiary venation pattern (char. 16) is unique to the Quiinaceae. In *Froesia*, *Lacunaria*, and *Touroulia*, the tertiary veins are densely spaced, strongly parallel, percurrent or, more frequently, anastomosing at different distances from their origin (e.g., Zizka & Schneider, 1999). In *Quiina* they are less parallel and more conspicuously branched, anastomosing with intersecondary or tertiary veins. This pattern is called plumose-reticulate according to Foster (1950a, b). A scalariform (ladder-like) pattern is observed in *Elvasia*.

Stipules. Stipules are always interpetiolar in Quiinaceae (char. 21), but the number of stipules or stipular lobes may differ among the genera (char. 22). Stipule number obviously varies with the phyllotaxis. In verticillate *Lacunaria* there is one stipule between neighboring petioles (as in verticillate *Q.*

Table 2. Data matrix of 61 morphological characters of the ingroup Quiinaceae and the outgroup, *Elvasia*, *Ouratea* (Ochnaceae), and *Medusagyne* (Medusagynaceae). In the matrix, inapplicable states are coded with a dash (-) and polymorphic taxa with letters: a = 0/1; b = 1/2; c = 0/2; d = 0/1/2; e = 2/3; ? = missing data.

Taxon	Character number						
	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	6 1
OCHNACEAE							
Elvasia calophyllea A. DC.	0000010001	000000υ00a	0-000000a0	00000d0000	0a00000020	0400000?0	1
Elvasia elvasioides (Planch.) Gilg	0000010000	0300000000	0-000000a0	00000d0000	0a00000000	0400000?0	0
Ouratea lucens (Kunth) Engl.	0000010002	110112000a	0-000010a0	000002a001	0000000020	1300000000	1
Ouratea parviflora (DC.) Baill.	00000a000d	0001120000	0-000010a0	000002a001	0000000020	1300000000	0
MEDUSAGYNACEAE							
Medusagyne oppositifolia Baker	0010010212	0011231000	2------100	0?00021000	0001011041	0000002000	0
QUIINACEAE							
Froesia diffusa Gereau & Rod. Vásquez	10111aa0aa	0200010000	1101001002	0000121211	0012011111	02a01010a0	1
Froesia tricarpa Pires	10111a00a2	a200010010	110100100b	0000121211	0012011111	02001010a0	1
Froesia venezuelensis Steyerm. & G. S. Bunting	1011110002	0200010000	110100100b	0000121211	0012011111	02001010a0	1
Lacunaria crenata (Tul.) A. C. Sm.	00200b0002	a2000100ab	12110013ab	01a0111210	0001021021	0101201101	0
Lacunaria decastyla (Radlk.) Ducke	002001a002	12000100a1	121a001311	020a111210	000102103?	0100201101	0
Lacunaria jenmanii (Oliv.) Ducke	00200ba00a	0300010 0ad	121a0013a1	c20a111210	a10a021031	01?0201100	0
Lacunaria macrostachya (Tul.) A. C. Sm.	00200b000a	03000100a1	1211001312	0200111210	1001021031	0100201100	0
Lacunaria oppositifolia (Pires) Pires	0a100100a0	0300010011	101a0013a2	01a01b1211	1a00011021	0101200101	0
Quiina amazonica A. C. Sm.	0110010011	010012000c	1011001211	2100011110	1000121001	01a0101100	0
Quiina cruegeriana Griseb.	011001201a	0100120011	1011001212	1100021110	1a0a121001	0100101110	0
Quiina florida Tul.	0110010000	0300120001	10a1a01211	220aa11b10	10001210a1	0101100101	0
Quiina guianensis Aubl.	01100b0011	0101120011	101a00121a	111a011110	100a121001	01001011a0	0
Quiina longifolia Spruce ex Planch. & Triana	0110010000	0301120011	1001101211	2100021110	1001121001	0110101100	0
Quiina macrophylla Tul.	0110010000	0300120001	1011001212	21000a11a0	100a121001	01001011a0	0
Quiina obovata Tul.	0a10020c0a	0102120012	1001001211	11100b1110	100a121001	01001011a0	0
Quiina oiapocensis Pires	0110020a0a	0100120012	100110b212	2200121210	1a01?21001	0110111101	0
Quiina paraensis Pires & Fróes	0110010010	0300120001	101100221b	1100111210	10011210b1	0101100100	0
Quiina pteridophylla (Radlk.) Pires	002002cc1b	0101120012	120111a211	b100120110	1000121001	0100101100	0
Quiina rhytidopus Tul.	01100a0000	0300120101	1011001211	2100011b10	100a121001	0110101100	0
Quiina tinifolia Planch. & Triana	0110010000	0300120011	1011001211	2b000a11a0	100a121001	0100101100	0
Touroulia amazonica Pires & A. S. Foster	00112000ab	a200010010	1011001?01	0?00121211	0001021021	0100201100	0
Touroulia guianensis Aubl.	00112a00a2	1200010010	1c1a001201	0b01121ba1	00010210e1	0100201100	1

pteridophylla). In opposite-leaved *Quiina* and *Lacunaria oppositifolia* there are four per node (paired between petioles), while in opposite-leaved *Touroulia* only two per node are observed. In the latter, this apparently single stipule is interpreted as a product of paired fusion similar to cases observed in Rubiaceae (Goebel, 1932). In opposite-leaved *Froesia*, the two stipules per node are deeply divided into setose lobes. In Quiinaceae, stipules are present on the terminal node at least. If stipules are generally lacking on the more basal nodes they are coded as caducous (char. 23); if generally present on the three uppermost nodes they are treated as persistent.

Flowers. Sex distribution (char. 28) is heterogeneous in Quiinaceae, with *Froesia* being bisexual, *Lacunaria* unisexual and dioecious, and *Quiina* and *Touroulia* morphologically androdioecious, with male and hermaphroditic flowers on different plants. The number of sepals (char. 36) is variable in Quiinaceae. Four sepals are common and usually constant for a species, while species with five or more sepals display a higher variability in number. Less than four sepals is an exceptional condition and therefore given its own state.

The hermaphroditic *Froesia* flower bears numerous stamens, frequently more than 100 (char. 44). In the androdioecious genera, the staminate flowers generally produce 30 to 80 stamens, whereas the hermaphroditic flowers normally produce fewer. For coding, only the flowers with functional stamens are included in the analysis. Character 45, filaments free or adnate to the petals, only refers to the hermaphroditic flowers of species of *Quiina* because in that genus staminate flowers do not show this trait. Concerning the gynoecium (char. 48), *Froesia* is clearly apocarpous while *Ouratea* is syncarpous, because apocarpy is only gained during fruit development (Amaral, 1991). In *Lacunaria* and *Touroulia* the number of carpels (char. 49) is variable and relatively high (4 to 14), while in *Quiina* there are commonly 2 carpels. In the latter, only a few species (e.g., *Quiina florida* Tul., *Q. paraensis* Pires & Fróes) show transitional states with up to 5 carpels.

Fruits. The exocarp is usually longitudinally striate to furrowed by underlying resiniferous lacunae that are more or less conspicuous in transection (char. 57). In *Quiina florida* and *Q. paraensis*, the exocarp appears quite smooth and is not striated by the lacunae. Additionally, their fruits are spotted by a substance that looks like dried resinous exudate (char. 54).

Crystalliferous cells. One characteristic feature is the presence of the cristarque cells (char. 61), a term introduced by van Tieghem (1902). These are crystal-bearing cells with a conspicuous u-shaped wall thickening. They are often cited in familial descriptions (Cronquist, 1981, as solitary crystals; Amaral, 1991; Bhattacharyya & Johri, 1998; Kubitzki, 1995 pers. comm.) and hence could be erroneously assumed to be characteristic for the entire family. So far we were able to confirm them only for the genera *Froesia* (*F. tricarpa* Pires, *F. venezuelensis*) and *Touroulia* (*T. guianesis*), in accordance with the findings of Foster (1950b). In addition to these specialized cells, crystal druses can be regularly observed in the leaf tissue (char. 60).

PHYLOGENETIC ANALYSIS

The data matrix in Table 2, containing 27 taxa and 61 characters, was analyzed with PAUP* 4.0 for Macintosh (Swofford, 1998), using the branch and bound algorithm under the assumption of Fitch parsimony (Fitch, 1971). Multiple character states were interpreted as uncertain. An initial search was undertaken with equal weights saving all optimal trees. To evaluate characters with the strongest phylogenetic signal and to choose among equally parsimonious trees (Carpenter, 1988, 1994), successive weighting analysis (Farris, 1969) was undertaken after the initial search. The settings used the rescaled consistency or RC index (Farris, 1989), and to avoid fractions the base weight was set to 1000. The process was reiterated until the same tree length was obtained twice. A similar analysis was carried out where characters 6 and 8 were ordered.

Branch stability was estimated with Bremer support and jackknife analysis for both the equally weighted and weighted characters. Bremer support is defined as the number of extra steps necessary to lose a clade in the consensus tree, using the converse constraints approach (Bremer, 1988, 1994; Källersjö et al., 1992; Farris, 1996). Reweighted and rescaled branch support values calculate the robustness for each branch in the weighted consensus tree (Bremer, 1994; Gustafsson & Bremer, 1995). To ease the construction of all necessary constraints, the computer program AutoDecay 4.0 was used (Eriksson, 1998). Each constraint was estimated with a heuristic search of 100 replicates of random additions of the taxa (10 repetitions of each replicate), tree bisection-reconnection (TBR) branch swapping, holding five trees at each step, and saving all equally parsimonious trees. Jackknife (Farris & al., 1996) investigates the structure, or phylogenetic signal, in a matrix with-

out permutation, contrary to bootstrap (Felsenstein, 1985), but excludes an assigned fraction of characters, here set to 35%. The search strategy was set as for the Bremer support, but with 1000 replicates and saving no more than 100 trees.

Results

The analyses using morphology to infer the phylogeny of Quiinaceae yielded 1643 most-parsimonious trees using all characters as unordered as well as when characters 6 and 8 were ordered. The trees are 163 steps long (when ordered 164 steps) with an RI of 0.775 and a CI of 0.561, or 0.529 when uninformative characters were excluded (Fig. 2). Counting steps within the polymorphic taxa, the trees are 282 steps long, indicating numerous polymorphic characters.

Successive weighting of the characters yielded a stable result of 2 trees after three iterations, 73.206 steps long using unordered characters. This tree is a subset of the initial 1643, resulting in a consensus with a much better resolution of the otherwise collapsed genera *Lacunaria* and *Quiina*. Consensus of the primary 1643 trees and the 2 trees obtained after successive weighting together with jackknife fractions, Bremer support values, and weighted and rescaled support values, are shown in Figure 2. One of the most-parsimonious trees with characters optimized on the branches is shown in Figure 3.

Referring to the unweighted analysis, Quiinaceae form a well-supported monophyletic group, a grade from *Froesia* at the base to the most derived genus *Quiina*. Within the family, all genera are monophyletic except for *Lacunaria*, a genus completely collapsed to a comb. Based on equally weighted characters, no resolution within *Quiina* can be retrieved. The small genus *Touroulia* forms the sister to the *Lacunaria–Quiina* complex. Support for *Froesia* and *Quiina* must be regarded as strong, while support for *Touroulia* is moderate. No clear signal for a monophyletic *Lacunaria* can be retrieved, and *L. oppositifolia* attaches as sister to *Quiina*, a position with low jackknife support of 54%, but not found in the consensus (Fig. 2).

As to the weighted analysis, resolution is improved and only one trichotomy remains, the one in *Froesia*. All clades found in the equally weighted analysis are retrieved and, as a general trend, moderately or strongly supported groups are often better supported after successive weighting. *Froesia*, supported by a maximum jackknife value in the equally weighted analysis, needs five extra steps to be lost when unweighted, a value twice as strong after successive weighting. A similar situation is observed for *Touroulia*, and the support for *Quiina* increases almost three times. Using the weighting approach, *Lacunaria* is now found to be monophyletic, although with a Bremer support of only 0.9.

Discussion

Because a cladistic analysis can only elucidate ingroup relationships, we cannot put forward a hypothesis of relationships within the order Malpighiales, or determine whether Quiinaceae are sister to a paired Medusagynaceae–Ochnaceae, or sister to either one separately. Support for Quiinaceae is strong, with little difference in support values between equally weighted and weighted characters. This implies that several characters are initially strong and basal on the tree; these non-homoplasious synapomorphies include pubescent stipules (char. 24: 1), pubescent sepals (char. 38: 2), heteromorphic sepals (char. 39: 1), and a fruit exocarp with lacunae (char. 55: 1; Fig. 3). Other synapomorphies for Quiinaceae, addressed in the introduction, are the unique leaf venation pattern with densely spaced parallel or plumose-reticulate tertiary veins (char. 16) and the interpetiolar stipules (char. 21: 1).

In a molecular study of the relationships of *Medusagyne oppositifolia* by Fay et al. (1997), Quiinaceae were represented by *Quiina pteridophylla*, *Touroulia guianensis*, and *Lacunaria jenmanii* (Oliv.) Ducke, all included in our study. Contrary to our results, *Quiina* was found to be the most basal taxon in the family. *Quiina pteridophylla* is a morphologically aberrant species within the genus with some characters resembling species of *Lacunaria*, such as the phyllotaxis and the stipule number. Therefore it may be an inappropriate representative of *Quiina* and could attach as sister to all other genera due to long-branch attraction.

Froesia is indicated by our cladistic analysis to be the most basal genus in Quiinaceae, followed by a grade of *Touroulia*, *Lacunaria*, and *Quiina*. Particularly noteworthy is the apocarpous gynoecium (char. 48) of *Froesia*, a character state known neither from other Quiinaceae nor from Ochnaceae or Medusagynaceae. However, some Ochnaceae exhibit a secondary—otherwise called "ecological" (Baum, 1951)—apocarpy during fruit development (Amaral, 1991). In her cladistic analysis, Amaral (1991) interpreted this secondary apocarpy as a derived state differing from the states observed in the Quiinaceae and Scytopetalaceae (both families therein used as outgroups). Whether apocarpy in *Froesia* evolved secondarily is difficult to infer. The existence of a compitum, providing support for the

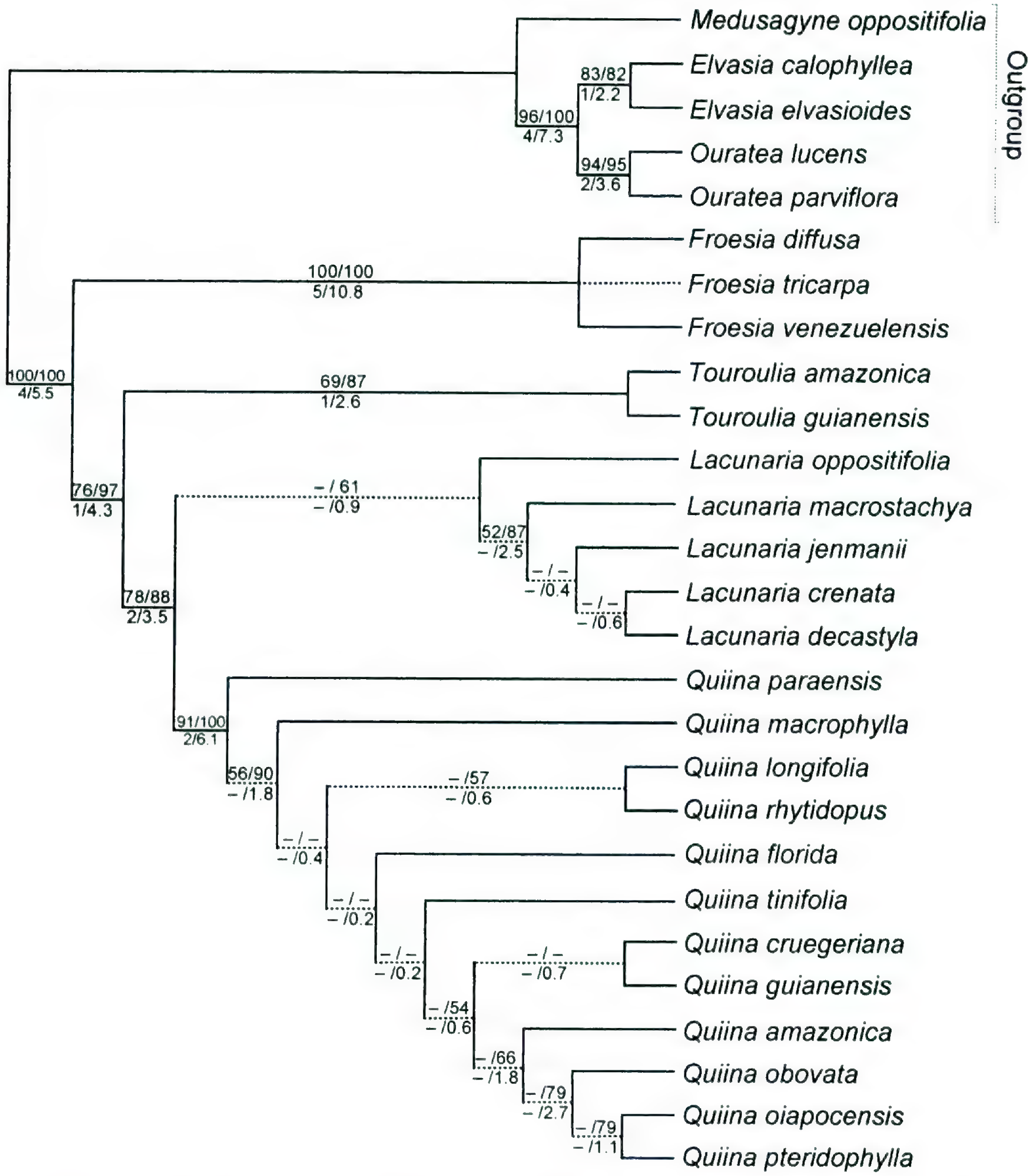

Figure 2. Strict consensus tree of Quiinaceae retrieved from a primary cladistic analysis applying equal weights to morphological characters (Tables 1 and 2), and a subsequent secondary analysis using successive weighting. The analyses yielded 1643 trees (163 steps, CI: 0.561, RI: 0.775) and two most-parsimonious trees, one a subset of the other. Dotted lines indicate collapsed branches in the primary analysis. Jackknife fractions above 50% using equal weights (left) as well as weighted characters (right) from the primary analysis are shown above the branches. Below branches are Bremer support values, i.e., additional steps needed to collapse a node for unweighted characters (left), and weighted and rescaled characters (right).

view that apocarpy is derived (see Endress, 1982; Kubitzki, 1995 pers. comm.), could not be observed. Nevertheless, according to the present analysis, this character state is considered a synapomorphy for *Froesia*.

The cladistic analysis indicates an isolated position for *Froesia* in terms of morphology. Support for the genus is strong with no less than eight synapomorphies (Fig. 3). These results correspond to the findings of Gottwald and Parameswaran (1967), who even proposed, based on anatomical studies, the establishment of a separate subfamily for *Froesia*. Besides the apocarpous gynoecium, deeply divided stipules with setaceous lobes (in all but one

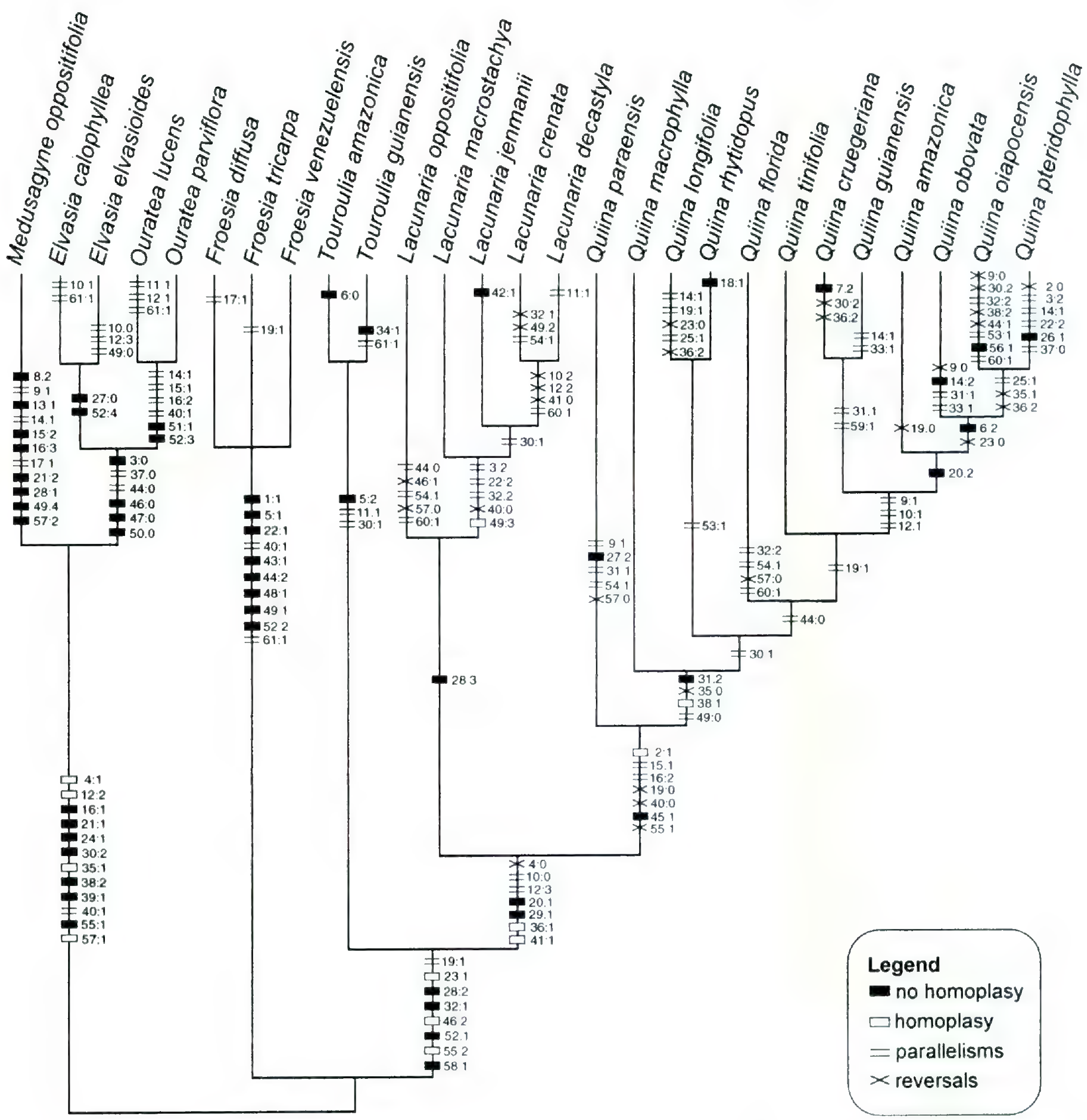

Figure 3. One of the two most-parsimonious trees from the successive weighting analysis of the Quiinaceae with characters optimized on the branches (number left of colon = character; right = character state, cf. Table 1).

species), glabrous seeds, and hermaphroditic flowers are important characters to distinguish the genus. This example addresses the importance of including autapomorphies in phylogenetic analyses, following Yeates (1992). If only one *Froesia* species had been included, a number of characters would have been regarded as autapomorphies, uninformative, excluded, and hence probably overlooked as potential synapomorphic characters for the genus.

Apart from *Froesia*, the remaining species of Quiinaceae are distinguished by several synapomorphies, including the evolution of staminate flowers (char. 28: 2), their position in small terminal groups (char. 32: 1), a berry-like fruit (char. 52: 1), and pubescent seeds (char. 58: 1). *Touroulia* forms a monophyletic group and is recognized by only one synapomorphy, the compound leaves with an alate rachis (char. 5: 2). As previously mentioned, generic rank was proposed for *T. amazonica* (Pires, in sched.), a view also advocated by Gottwald and Parameswaran (1967) based on their anatomical studies. Nevertheless, from a morphological point of view, the two *Touroulia* species are very similar (Zizka & Schneider, 1999), confirmed by the present analysis, and, hence, Pires's proposal is rejected.

A number of characters unite the genera *Quiina*

and *Lacunaria.* Polymorphic characters such as the position of the inflorescence (char. 29) in *Lacunaria* are interpreted as inconclusive of relationship (soft starts sensu Kornet and Turner, 1999). Regarding *Lacunaria,* conflicting data fail to conclusively resolve the taxa in the analysis using equal weights, but support for *Quiina* is strong. However, a phylogenetic signal for *Lacunaria* is picked up if the approach to character weighting is used, gaining a fully resolved tree, but with very low support values. A jackknife value of 61% and a rescaled Bremer support value of 0.9 cannot be considered as much support for a monophyletic genus. Based on the weighted analysis, a possible single synapomorphy is identified for *Lacunaria* (char. 28: 3). Most other characters are homoplastic within the genus, and some are also observed in, for example, *Quiina pteridophylla.* Our knowledge of interrelationships within *Lacunaria* is not satisfactory, but pending future analysis we refrain here from proposing any systematic rearrangement and treat the genus in its traditional circumscription.

Two characters, verticillate leaves (char. 3: 2) and completely fused stipules (char. 22: 2), have evolved in the clades of *Lacunaria* and *Quiina.* Based on our morphological studies, *Quiina pteridophylla* was expected to be closely related to *Lacunaria.* The present analysis indicates that *Q. pteridophylla* shares almost all other generic characters and that it is deeply nested within *Quiina* rather than having a basal position in the genus. Forcing a sister relationship of *Q. pteridophylla* with *L. oppositifolia,* which it superficially resembles, costs no less than 10 extra steps. Thus, there is no doubt that these two species are not closely related and cannot form a sister relationship.

Reasons for previous hypotheses of recognizing *Lacunaria oppositifolia* at generic rank can here be understood. Following the weighted analysis and tracing character evolution (Fig. 3), the species forms a clearly distinct branch with no less than five homoplastic characters. The remaining lineage of *Lacunaria* has, interpreted from the tree in Figure 3, gained the same number of homoplastic characters, although they are different. Although a monophyletic genus can be envisioned, there is also weak jackknife support for *L. oppositifolia* forming a separate lineage nested between *Lacunaria* s. str. and *Quiina* if equal weights are used. One option is to include *L. oppositifolia* in *Quiina,* but this solution is not attractive because a morphologically well circumscribed group would be lost. Leaf venation pattern, the absence of intersecondary veins, and the number of carpels do not coincide with the generic concept of *Quiina.* Moreover, cladistic support of the genus *Quiina* is almost four times as strong as the next internal node. A second solution is to describe a monotypic taxon, but due to the weak support, and not appearing in the consensus, the issue of the rank and position of *L. oppositifolia* has to be postponed until other data, particularly from DNA analyses, are obtained.

Taxa sampled of *Quiina* for this analysis include about one third of the total number of the species. As a genus, *Quiina* is rather well supported, but support clearly increases after successive weighting. A cursory inspection of Figure 3 also reveals a number of reversals and parallelisms on branches leading to the terminals, especially in the most advanced part of the tree. We interpret this, in conjunction with a high ratio of polymorphic characters, to indicate that novelties are allowed to rise and spread within the lineage. They represent soft reversals without hard starts of character states (Kornet & Turner, 1999). Two reasons, and possibly more, explain this observation. First, the lineage might be fairly young and presently going through numerous speciation events without character state fixation. Second, interpretations of our character states may be incorrect, i.e., misinterpretation of homologies.

EVOLUTION OF ANDRODIOECY

Different modes of sex distribution in the Quiinaceae—androdioecy in *Quiina* and *Touroulia,* dioecy in *Lacunaria*—seem to have evolved from a hermaphroditic ancestor. Hermaphroditism is the plesiomorphic state, found in the basal genus *Froesia* and in the outgroup Ochnaceae. Andromonoecy is an autapomorphy for the outgroup taxon *Medusagyne* and is not further considered herein. Androdioecy (char. 28: 2) is a synapomorphy within Quiinaceae that evolved, in a phylogenetic perspective, in the following pathway: androdioecy is the plesiomorphic state and dioecy independently evolved in *Lacunaria.*

Concerning the evolution of androdioecy and dioecy, several models have been formulated (Ross, 1978, 1982; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Swensen et al., 1998). The majority regards dioecy as derived from hermaphroditism via androdioecy or gynodioecy (Darwin, 1877; Westergaard, 1958; Bawa, 1980; Richards, 1997). Another model of androdioecy evolution proposed by Ross (1982) is from hermaphroditic flowers via andromonoecy, as observed in some *Solanum* species. However, andromonoecy is only known from the outgroup, *Medusagyne.* In contrast, Swensen et al. (1998) ar-

gued that [functional] androdioecy evolved from dioecy in Datiscaceae. This path is improbable for Quiinaceae since androdioecy evolved once in the ancestor of *Touroulia*, *Lacunaria*, and *Quiina*, with a further reduction to dioecious flowers in *Lacunaria*.

Mechanisms that favor the evolution of androdioecy and dioecy are explained by models of sexual selection and sex allocation, and are discussed by several authors (Ross, 1978, 1982; Bawa, 1980; Thomson & Barrett, 1981; Charlesworth, 1984; Thomson & Brunet, 1990; Richards, 1997; Pannell, 1997). One hypothesis argues that in female-sterile plants the loss of seed production is more than compensated for by the reallocation of resources to increased pollen production (Thomson & Brunet, 1990). This may be achieved through an increased number of staminate flowers or stamens, or through larger anthers. Flower numbers are more or less equal among the Quiinaceae or even lower in the (andro-)dioecious taxa. Anthers are roughly of the same size in the family, hence not serving as a useful argument. The number of stamens, indeed, is generally increased in staminate flowers of *Quiina* and *Touroulia*. Nevertheless, comparing the genera, the stamen numbers do not provide an explanation for the evolution of the observed pattern of sex distribution since the supposedly ancestral hermaphroditic flowers of *Froesia* bear the highest number of stamens within the family. If we trace an evolutionary pathway from hermaphroditism through androdioecy to dioecy, as postulated above, we see a reduction of stamen numbers from more than 100 in *Froesia*, 30 to 80 in *Touroulia*, most *Lacunaria*, and some of the *Quiina* species, to approximately 10 to 25 in *Quiina* and in a few *Lacunaria* species, including *L. oppositifolia*. Thus, other mechanisms such as the avoidance of inbreeding may provide a better explanation for the evolution of dioecy in the present case.

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A REVIEW OF THE GENERA *ROENTGENIA* AND *POTAMOGANOS* (BIGNONIACEAE)[1,2]

Warren D. Hauk[3]

Abstract

Roentgenia and *Potamoganos* (Bignoniaceae) are small genera of lianas with "*Cydista*-type" corollas that are closely related to larger and more well known genera such as *Cydista*, *Clytostoma*, and perhaps *Phryganocydia*. *Roentgenia* is ditypic, containing *R. bracteomana* and *R. sordida*, whereas *Potamoganos* is monotypic, containing only *P. microcalyx*. The two species of *Roentgenia* have white to lavender, campanulate-funnelform, *Cydista*-type corollas, stems with eight phloem arms, bi-trifid tendrils, 3(–4)-colpate pollen with reticulate exine, 2-seriate ovule organization, nectariferous disk lacking, linear-oblong fruit, and winged seeds. *Roentgenia bracteomana* is distributed from southern Colombia to northern Bolivia and north-central Brazil, whereas *R. sordida* is restricted to eastern Venezuela, Guyana, Suriname, French Guyana, and portions of northern Brazil. *Potamoganos microcalyx* has lavender to magenta, campanulate-funnelform, *Cydista*-type corollas, with four phloem arms, trifid tendrils, 3-colpate pollen with reticulate exine, 4-seriate ovule organization, and a nectariferous disk. *Potamoganos microcalyx* is known from southern Venezuela, Guyana, Suriname, and northernmost Brazil. A key to species, maps of species distributions, reproductive phenology, and illustrations of *R. bracteomana* and *P. microcalyx* are provided.

Key words: Bignoniaceae, Bignonieae, *Cydista*, *Potamoganos*, *Roentgenia*.

Roentgenia (K. Schum. ex Sprague) Urb. and *Potamoganos* Sandw. (Bignoniaceae) belong to tribe Bignonieae, which is composed almost exclusively of lianas and which has been demonstrated recently to be monophyletic using *rbc*L and *ndh*F gene sequences (Spangler & Olmstead, 1999). *Roentgenia* is a ditypic genus of primarily lowland lianas with white to lavender, campanulate-funnelform, "*Cydista*-type" corollas (Fig. 1), stems with eight phloem arms, bi-trifid tendrils, 3(–4)-colpate pollen with reticulate exine, 2-seriate ovule organization, nectariferous disk lacking, linear-oblong fruit, and winged seeds (Gentry, 1977, 1978, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished). *Roentgenia* is closely related to such genera (Table 1) as *Cydista* Miers (6 species), *Clytostoma* Miers ex Bureau (12 species), *Potamoganos* (1 species), and *Phryganocydia* Mart. ex Bureau (4 species) (Gentry, 1977, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished; Hauk, 1997).

Potamoganos is a monotypic genus of primarily lowland lianas with lavender to magenta, campanulate-funnelform corollas (Fig. 2). Among genera of tribe Bignonieae with "*Cydista*-type" flowers, it is distinguished by a combination of characters: stems with four phloem arms, trifid tendrils, 3-colpate pollen with reticulate exine, 4-seriate ovule organization, and a nectariferous disk (Gentry, 1977, 1978; Gentry & Tomb, 1979; Tomb & Gentry, unpublished; Hauk, 1997). *Potamoganos* has a "*Cydista*-type" corolla (Gentry, 1978) and is closely related to several larger genera (Table 1) such as *Cydista*, *Clytostoma*, *Roentgenia*, and *Phryganocydia* (Gentry & Tomb, 1979; Hauk, 1997).

The late Alwyn H. Gentry treated *Roentgenia* and/or *Potamoganos* in several regional floras (Gentry, 1977, 1978, 1983, 1993, 1997, in press), but his monographic work did not encompass *Roentgenia*, *Potamoganos*, or other genera of the tribe Bignonieae. This paper utilizes the vast amount of information chronicled by Gentry in his studies of Bignoniaceae and attempts to compile these sources on *Roentgenia* and *Potamoganos* into a single treatment. The database established by Gentry's investigations has allowed production of detailed maps of geographic distribution (Figs. 3, 4). Distribution data presented here provide an important foundation for future investigations of the

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Table 1. Morphological/anatomical characters and character states for *Roentgenia* and *Potamoganos* and three genera putatively closely related (after Gentry, 1977, 1997; Gentry & Tomb, 1979; Tomb & Gentry, unpublished).

	Tendrils	Phloem arms	Nectar disk	Corolla pubescence	Ovule organization	Fruit surface	Seed	Pollen aperture	Pollen exine
Roentgenia	bi-trifid	8	absent	lepidote	2-seriate	non-echinate	bialate	3(–4)-colpate	reticulate
Cydista	simple	8	absent	lepidote	2(–4)-seriate	non-echinate	bialate	inaperturate/pericolpate	reticulate
Clytostoma	simple	8	absent	lepidote	2(–4)-seriate	echinate	corky	inaperturate	reticulate
Phryganocydia	simple	8	absent	lepidote	2-seriate	non-echinate	corky	inaperturate	reticulate
Potamoganos	trifid	4	present	glabrous/lepidote	4-seriate	?	?	3-colpate	reticulate

taxonomy and systematics of *Roentgenia* and *Potamoganos*.

History and Systematics

In 1916, Urban described *Roentgenia* and transferred *Cydista bracteomana* K. Schum. ex Sprague into the genus as its sole species. Urban considered *Roentgenia* distinct from *Cydista* based on the trifid tendrils and plurisulcate pollen of the former (Sprague & Sandwith, 1932). Sprague and Sandwith transferred *Arrabidaea sordida* Bureau & K. Schum. to *Roentgenia* in 1932, after examining additional collections more complete than the holotype. Macbride (1961) questioned the use of pollen characters alone as generic markers, and noted that other characters, for example simple vs. trifid tendrils, that separate *Roentgenia* from *Cydista* are not stable in Bignoniaceae. Gentry (1974a) acknowledged that the primary features distinguishing the two genera, tendril and pollen, might not be sufficient to retain *Cydista* and *Roentgenia* as distinct. Gentry (1978: 262) wrote that *Roentgenia* is "barely separable from *Cydista*," although he treated them as distinct in his floristic works (Gentry, 1977, 1978, 1983, 1993, 1997).

Gentry (1974a: 880) reported that the distinction between the trifid tendril of *Roentgenia* and the simple tendrils of *Cydista* "breaks down" in a collection of *R. bracteomana* (*Seibert 2146*; not examined by this author). However, the putative presence of anomalous tendrils in a single specimen does not provide a strong argument for treating *Roentgenia* and *Cydista* as congeneric. From a cladistic perspective, the perisyncolpate pollen, linear to linear-trisect bracts and bracteoles, and trifid tendrils of *R. bracteomana* and *R. sordida* provide synapomorphies that indicate they are sister species. Because there is no evidence, either morphological or molecular, that provides a sound basis for combining the two genera, this treatment retains *Roentgenia* as distinct from *Cydista*. Whether *Roentgenia* arose from within a paraphyletic *Cydista* (or conversely), or as sister to *Cydista* or another closely related genus, is not clear at this time. Only future, detailed morphological and/or molecular investigations will be able to address rigorously the monophyly of *Roentgenia* and *Cydista*, and the relationship of these two genera to the presumably closely related *Clytostoma*, *Phryganocydia*, and *Potamoganos*.

G. F. W. Meyer described *Bignonia microcalyx* in 1818, and Sandwith (1937) transferred it to *Potamoganos*, noting its affinities to *Cydista* and *Roentgenia*. However, Sandwith (1937) asserted

that the presence of a nectariferous disk distinguished the taxon from both *Cydista* and *Roentgenia*.

The cupular calyx and "*Cydista*-type" flower of *Potamoganos* (Fig. 2A) led Gentry (1978) to conclude that *Potamoganos* is allied to *Cydista* and *Roentgenia*. However, *Potamoganos* differs from these genera in having a well-developed nectariferous disk (Fig. 2C), and lacking glandular fields [presumably on the calyx] (Gentry, 1978). Three other genera, *Clytostoma*, *Roentgenia*, and *Phryganocydia*, possess the "*Cydista*-type" corolla but lack a nectariferous disk (Gentry, 1978). However, *Phryganocydia* has a long, spathaceous calyx, not the cupular calyx characteristic of *Roentgenia* and *Cydista*.

The 3-colpate pollen of *Potamoganos* differs from the inaperturate pollen of *Clytostoma*, *Phryganocydia*, and most species of *Cydista* (Gentry & Tomb, 1979). *Roentgenia* is the only other genus with *Cydista*-type corollas that has aperturate pollen (i.e., colpate), although perisyncolpate pollen is known in four of the six species of *Cydista* (*C. decora*, *C. diversifolia*, *C. heterophylla*, and *C. aequinoctialis*; Gentry & Tomb, 1979). The surface of *Roentgenia* pollen is verrucate to scabrate, and unlike the medium-reticulate surface found in *Potamoganos* pollen (Gentry & Tomb, 1979). *Phryganocydia* has finely scabrate pollen that differs from the medium-reticulate type of *Potamoganos*, *Clytostoma*, and most species of *Cydista* (Gentry & Tomb, 1979).

The chromosome numbers of *Roentgenia* and *Potamoganos* are not known. However, Goldblatt and Gentry (1979) reported chromosome numbers of $2n = 40$ in 21 of the 23 genera of tribe Bignonieae they surveyed, including *Cydista* and *Clytostoma*, and it is likely that *Roentgenia* and *Potamoganos* have a similar chromosome number.

Distribution

Collections of *R. bracteomana* extend from southern Colombia to northern Bolivia, with some extension into north-central and western Brazil (Fig. 3). Collections of *R. sordida* occur from eastern Venezuela, Guyana, Suriname, French Guiana, and northern Brazil, with a single collection from Amazonas, Brazil (Fig. 3).

Collections of *Potamoganos microcalyx* occur from south-central Venezuela, Guyana, Suriname, and the northernmost portions of Brazil (Fig. 4). In western Suriname, *P. microcalyx* grows in lowland forests (0–60 m) and is present in many moist forests and riverine habitats (pers. obs.).

Phenology

Roentgenia and *Potamoganos* are closely related to a group of genera (*Cydista*, *Clytostoma*, and *Phryganocydia*) that Gentry and Tomb (1979) suggested constitute a natural group because they share similar pollen morphology, a tendency toward "multiple bang" flowering phenology, and the absence of a nectariferous disk. "Multiple bang" species have numerous, synchronized, short flowering periods (ca. 3 days) that may occur at any time of the year (Gentry, 1974b). The absence of a nectariferous disk (and presumably nectar), coupled with conspicuous visual and olfactory attractants, indicates that pollinator deceit may be the ultimate pollination strategy (Gentry, 1974b). The short, repeated floral bursts may serve to lure novice pollinators that effect pollination through visits to only a few flowers, after which they seek a more ample nectar source (Gentry, 1974b). Visits by potential pollinators are infrequent, presumably because pollinators learn quickly that the flowers offer no nectar reward (Gentry, 1974b).

Fertile collections of *Roentgenia bracteomana* and *R. sordida* are known from throughout the year and are consistent with a "multiple bang" pollination syndrome. However, little is known about the pollinators of these two species, and more detailed examinations of flower production are necessary to document reproductive mode.

The reproductive biology of *Potamoganos* is not documented, but the close relationship of *Potamoganos* to "multiple bang" genera suggests a predisposition to a "multiple bang" strategy. However, the nectariferous disk in *Potamoganos microcalyx* (Fig. 2C) could signal a departure from the "multiple bang" strategy. The flowering specimens examined for this treatment document that *P. microcalyx* flowers in February, April, May, and October. Thus, the phenology data available are consistent with a "multiple bang" syndrome for *P. microcalyx*.

Materials and Methods

Gentry compiled a private database of label information from herbarium specimens he collected and from specimens at other herbaria that he examined personally. Gentry's database has been incorporated into the Missouri Botanical Garden database-management system, TROPICOS, which also contains label information for all *Roentgenia* and *Potamoganos* specimens housed at MO. All types were assumed to have been seen by Gentry unless otherwise noted. Gentry did not always designate types as "holotype," "isotype," or "syntype," and the designations presented here are based upon

inferences drawn from Gentry's work and the original literature; these type designations were not based on personal verification of specimens at the various herbaria. An index to numbered exsiccatae is provided in Appendix 1.

Data used for mapping and phenology were downloaded from TROPICOS, <http://mobot.mobot.org/W3T/Search/vast.html>. For records with no latitude/longitude coordinates in TROPICOS, approximate coordinates were obtained from gazetteers produced by the U.S. Board on Geographic Names, Office of Geography, Dept. of the Interior. Distribution maps were produced using the computer program VERSAMAP 1.51 (C. H. Culberson, Newark, DE, 1991–1995).

TAXONOMIC TREATMENT

Roentgenia Urb., Ber. Deutsch. Bot. Ges. 34: 747. 1916. TYPE: *Roentgenia bracteomana* (K. Schum. ex Sprague) Urb.

Lianas; stems terete to subtetragonal with 8 phloem arms in cross section; branchlets terete to subtetragonal with interpetiolar glandular fields lacking and transverse interpetiolar ridges present or absent, the younger branchlets striate, glabrate to lepidote; pseudostipules caducous to somewhat persistent, foliaceous, chordate-orbicular, glandular, glabrate to lepidote. *Leaves* opposite, estipulate, petiolate, bifoliolate with the terminal segment often modified into a trifid tendril; petioles and petiolules terete to slightly flattened, glabrate to puberulent or sparsely lepidote; ultimate segments entire, chartaceous, marginally plane; venation brochidodromous; midrib prominent with secondary veins pinnate; axils of secondary veins lacking glandular fields. *Inflorescences* elongate, axillary or terminal racemes, branched or unbranched, several- to many-flowered; rachis and peduncles terete to subtetragonal, puberulent to lepidote, and bracteate, the bracts linear to linear-trisect, each segment linear, persistent to caducous, glandular or eglandular, puberulent to caducous; pedicels terete, puberulent to lepidote; bracteoles linear to linear-trisect, persistent to caducous, glandular or eglandular, puberulent to lepidote. *Flowers* ovoid in bud; calyx campanulate-funnelform, glandular or eglandular, costate or ecostate, glabrate to lepidote or puberulent, the calyx margin usually split, apically truncate except for five minute teeth; corolla zygomorphic, tubular-funnelform, white to magenta with purple markings and the tube yellowish, glabrate to lepidote externally, pilose pubescence at the base of the filaments; corolla lobes 5 (2 upper and 3 lower), short-orbicular, the inner surface glabrate to lepidote, the outer surface lepidote; stamens 5, fertile stamens didynamous with the fifth stamen modified into a staminode, all adnate to the corolla; fertile anthers with two spreading thecae, included, glabrate; disk absent; ovary cylindrical, lepidote, the ovules biseriate in each locule; stigma included, bipartite, the divisions laterally flattened. *Fruit* a septicidal capsule dehiscing parallel to the septum, linear-oblong, the valves compressed and not conspicuously thickened, the margins not serially constricted, drying brown, the midline not evident, the surface rough, plane and glabrescent or sparsely lepidote to puberulous; many-seeded; seeds flattened, oblong, bialate, the body distinct and bipartite.

KEY TO FLOWERING SPECIMENS

1. Bracts 10–15 mm long; bracteoles 5–10 mm long, extending beyond the base of the calyx .... *R. bracteomana*

1'. Bracts 1–5 mm long; bracteoles 1–3 mm long, not extending to the base of the calyx .... *R. sordida*

1. Roentgenia bracteomana (K. Schum. ex Sprague) Urb., Ber. Deutsch. Bot. Ges. 34: 747. 1916. *Cydista bracteomana* K. Schum. ex Sprague, Verh. Bot. Vereins Prov. Brandenburg 1908: 121. 1909. TYPE: Brazil. Amazonas: Victoria, Rio Jura, May 1901, *Ule 5497* (holotype, B not seen; isotypes, HB not seen, L not seen, MG not seen). Figure 1.

Lianas; branchlets drying light brown to gray, terete to subtetragonal, with interpetiolar transverse ridge evident but inconspicuous, the lenticels not evident or inconspicuous; pseudostipules caducous, 8–11 × 15–18 mm. *Leaves* 10–37 cm long; petioles 0.5–6.0 cm, terete to slightly flattened, glabrate to sparsely lepidote; petiolules 1.0–5.0, terete, glabrate to lepidote; ultimate segments (7)10.5–28 × 4.5 × 14 cm elliptic to ovate-elliptic, densely lepidote when young, in older leaves glabrescent to sparsely and inconspicuously lepidote, especially along the basal portions of the veins beneath, apically acute, basally acute to obtuse, with 5–6 principal vein pairs. *Inflorescences* axillary racemes to 30 cm long, unbranched, several- to many-flowered; rachis and peduncles terete to subtetragonal, lepidote, and bracteate, the bracts trisect, each segment linear, 10–15 × 2–4 mm, persistent, glandular, lepidote; pedicels 5–7 mm long, lepidote; bracteoles 5–10 × 1–3 mm, persistent, glandular or eglandular, lepidote, extending beyond the base of the calyx. *Flowers:* calyx 5–10 × 4–7 mm, glandular or eglandular, costate, the outer calyx surface sparsely lepidote, the inner surface glabrate, the margin intact or split 1/4–1/2 the length of the tube, the valves apically

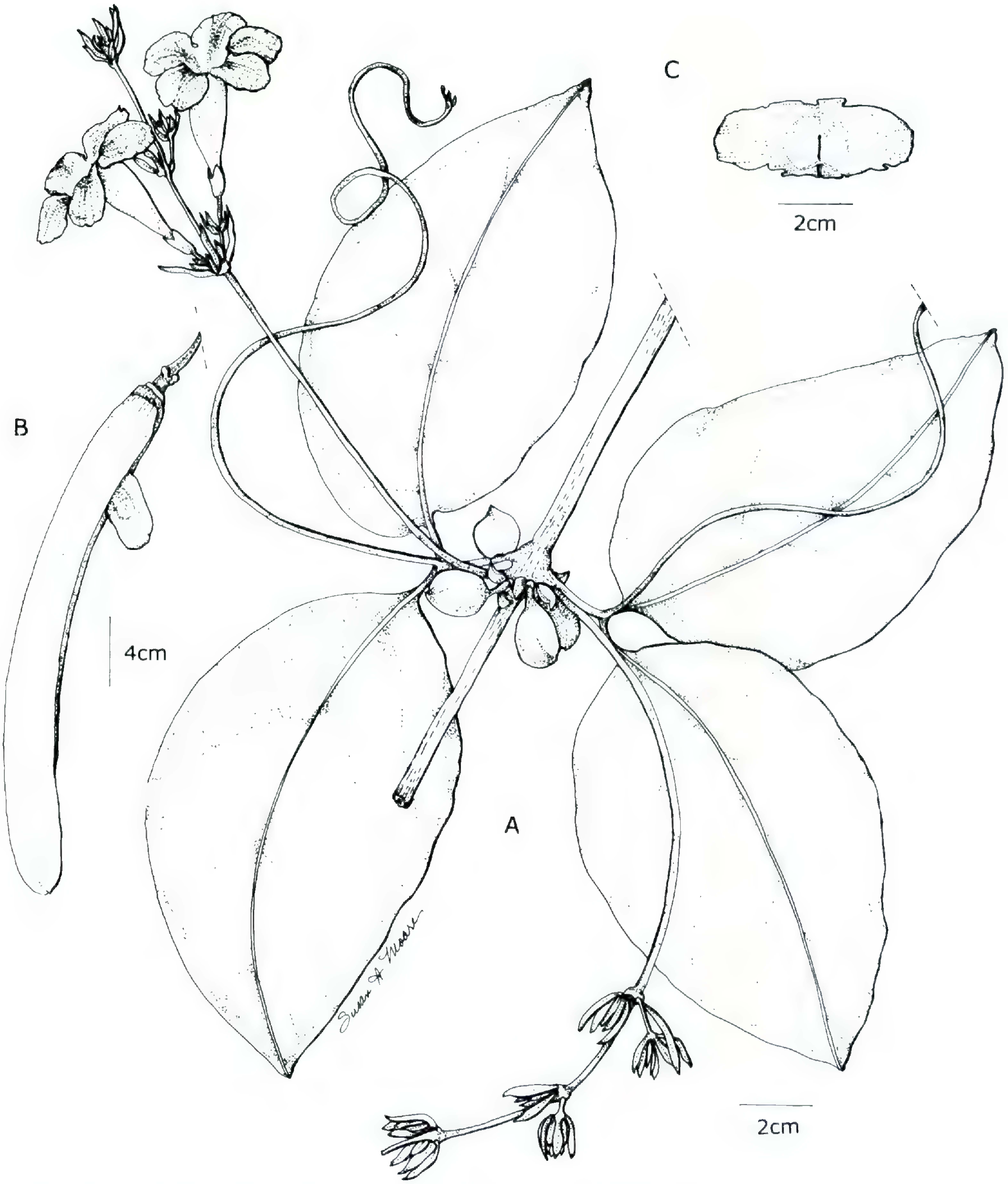

Figure 1. *Roentgenia bracteomana*.—A. Leaves with inflorescence, after *R. Burnham 1563*.—B. Fruit with seed, after *Plowman & Schunke V. 7503*.—C. Seed, after *Plowman & Schunke V. 7503*.

acute to truncate except for 5 minute teeth; corolla exserted 30–35 mm beyond the calyx lip (35–40 mm total length), 2–3 mm wide at the calyx lip; corolla lobes 15 × 10 mm; fertile stamens 9 or 16 mm long, inserted ca. 10 mm beyond the corolla tube base, the staminode 2 mm long, inserted 2 mm proximal to the stamens; ovary 2–3 mm long; style ca. 30 mm long. *Capsule* 27–60 × 2.0–2.5 mm, glabrescent; seeds flattened, 2.0–2.3 × 5.5–6.2 cm, 1–2 mm thick, oblong, bialate, the body ovoid and bipartite. *Figure:* Gentry (1993, fig. 71–6).

Distribution, elevation, and habitat. Known from southern Colombia to northern Bolivia with a few collections from western and north-central Brazil (Fig. 3). Collections are reported from 150 to

870 m, in premontane wet and tropical wet forests, on terra firme forests or in riverine habitats.

Phenology. Flowering collections of *Roentgenia bracteomana* are from: January (10), February (4), March (4), April (1), May (3), July (1), August (3), September (1), October (7), November (1), and December (1). Fruiting collections are from: February (1), March (1), April (1), May (3), June (4), July (3), September (2), and October (3).

Representative specimens. COLOMBIA. **Caquetá:** 41 km N of Florencia, 1060 m, *Gentry 9169* (MO). **Putumayo:** Selva higrofila del Río Putumayo en las márgenes del afluente izquierda La Concepción, 225 m, *Cuatrecasas 10834* (COL). ECUADOR. **Napo:** Armenia Vieja at Río Napo, 12 km SW of Coca, *Lugo 2703* (GB, MO). **Morona-Santiago:** Taisha, Río Guaguaine, 500 m, *Cazalet & Pennington 7558* (K, NY, US). **Pastaza:** Río Bobonaza, Quilloallpa below Montalvo, 02°10′S, 76°53′W, 300 m, *Øllgaard et al. 34586* (AAU, MO). **Santiago-Zamora:** banks of Río Guaguaymi, 500 m, *Cazalet & Pennington 7558* (K, NY, US). **Sucumbios:** without exact locality, 240 m, 00°08′S, 76°22′W, *Carlos E. Cerón & Judith Ayala 9469* (MO). **Zamora-Chinchipe:** without exact locality, 930 m, 04°18′S, 78°43′W, *W. Palacios, I. Vargas & E. Freire 8717* (MO). PERU. **Amazonas:** Armango, 300 m, *Woytkowski 5637* (MO). **Huánuco:** Codo de Pozuzo, alluvial fan floodplain of Río Pozuzo, 10°15′S, 74°55′W, 300 m, *Foster 9388* (MO). **Loreto:** Alto Amazonas, Río Pastaza, Lago Rimachi, 04°20′S, 76°35′W, 200 m, *Díaz S. & Ruiz 924* (AAU, MO). **Madre de Dios:** 39 km SW of Pto. Maldonado, Laguna Cocacocha, 12°50′S, 69°20′W, *Smith & Shuhler 400* (MO). **Puno:** ridge between Río Candamo and Río Guacamayo, 13°30′S, 69°50′W, 400–600 m, *Gentry et al. 76941* (MO). **San Martín:** Fundo San Pablo, Mariscal Caceres, Tocache Nuevo, 450 m, *Schunke V. 11788* (F). **Ucayali:** vicinity of LSU base camp, Quebrada Shesha, ca. 65 km NE of Pucallpa, 08°02′S, 73°55′W, 250 m, *Gentry & Díaz 58505* (MO). BOLIVIA. **Beni:** Km 34 carretera Yucumo–Rurrenabaque, Colegio Técnico Agropecuario Río Colorado, 14°50′S, 67°05′W, 230 m, *Smith et al. 14115* (MO). **La Paz:** Abel Iturralde Province, Alto Madidi across from mouth of Río Enlatagua, 13°35′S, 68°46′W, 280 m, *Gentry & Estensoro 70344* (MO). BRAZIL. **Amazonas:** Rio Jurua, *Ule, E. 5497* (HB, L, MG). **Maranhão:** Rio Xingu, 04°49′S, 52°31′W, *Balée 1958* (NY).

Flowering material of *Roentgenia bracteomana* is distinctive because of the prominent bracts and bracteoles; no species of *Cydista* or *Clytostoma* have similar-sized bracts or bracteoles. The lack of conspicuous bracts and bracteoles in *R. sordida*, coupled with a largely allopatric distribution, makes confusion of the two species unlikely. Vegetatively, trifid tendrils distinguish *Roentgenia* from *Cydista* and *Clytostoma*, but sterile material lacking tendrils may be easily mistaken for species of these closely related genera.

2. **Roentgenia sordida** (Bureau & K. Schum.) Sprague & Sandw., Bull. Misc. Inform. Kew 1932: 91–92. 1932. *Arrabidaea sordida* Bureau & K. Schum., in Mart., Fl. Bras. 8 pt. 2, fasc. 118: 30–31. 1896. TYPE: Guyana. Upper Rupunini River, *Schomburgk 1296* (holotype, B not seen, presumed destroyed).

Arrabidaea pullei Sprague, Bull. Herb. Boissier, 2 ser. 6(5): 373–374. TYPE: Suriname. Sipaliwini: upper Saramacca River, *Pulle 170, 495* (holotype, U not seen).

Lianas; branchlets drying tan to gray, terete, glabrate to puberulent or lepidote, with transverse interpetiolar ridge evident but inconspicuous, the lenticels not evident; pseudostipules ± persistent, foliaceous, 5–8 × 6–7 mm. *Leaves* 11–27 cm long; petioles 1.2–5.0 cm, terete, puberulent; petiolules 0.6–3.0 cm, terete, puberulent; ultimate segments 8–22 × 3–15 cm, elliptic to ovate, glabrate to lepidote (especially on young material) or puberulent, especially on basal portions of the main veins, apically acute to obtuse, basally obtuse to rounded or inequilateral, with 5 to 6 principal vein pairs. *Inflorescences* axillary or terminal racemes to 20 cm long, unbranched, many-flowered; rachis and peduncles terete to subtetragonal, puberulent to lepidote, bracteate, bracts 1–5 × 0.5–1 mm, caducous, eglandular, puberulent to lepidote; pedicels 3–6 mm long, puberulent to lepidote; bracteoles linear (to linear-trisect), 1–3 × 0.5–1.0 mm, caducous, eglandular, puberulent to lepidote, not extending to the base of the calyx. *Flowers*: calyx 4–7 × 3–6 mm, glandular, ecostate, the outer calyx surface puberulent to lepidote, the inner surface glabrate, the margin intact or split 1/8–1/2 the length of the calyx, the valves apically obtuse with 5 minute teeth; corolla exserted (25)32–42 mm beyond the calyx lip ((29)36–49 mm total length), 1.5–3 mm wide at the calyx lip; corolla lobes 12 × 12 mm; fertile stamens 8 or 16 mm long, inserted 9 mm beyond the corolla tube base, the staminode 2 mm long, inserted 1–2 mm proximal to the insertion of the fertile stamens; ovary 4 mm long; style ca. 25 mm long. *Capsule* 27–34 × 2 mm, sparsely lepidote to puberulous; seeds not observed. *Figures:* Gentry (1983, fig. 39; 1997, fig. 409).

Distribution, elevation, and habitat. Known from eastern Venezuela, Guyana, Suriname, French Guiana, and northern Brazil, with a few, scattered collections from western Brazil (Fig. 3). Collections are reported from 350 to 2000 m, in non-inundated moist forests, swampy mature forests, or white sand areas.

Phenology. Flowering collections of *Roentgenia sordida* are from: January (5), March (1), April (1), May (3), July (1), September (1), October (6), November (7), and December (4). The sole fruiting specimen examined was collected in March.

Representative specimens. BRAZIL. **Amapa:** Mpio. de Calcoene, 02°49′N, 51°23′W, *S. Mori & R. Souza 17263* (MO). **Amazonas:** São Paulo de Olivença, basin creek of Belém, *Krukoff 8623* (BM, F, MO, NY, U). **Maranhão:** Monção, P.I. Guaja, Rio Turiaçú, 03°07′S, 46°0′W, *Balée 3517* (MO). **Pará:** Campus of IPEAN, Belém, *Gentry 13077* (MO). FRENCH GUIANA. Approuague, en amont de Crique Tortue, *Oldeman 2303* (CAY). **Cayenne:** Montagne de Kaw, Piste Roura/Kaw, 04°33′N, 52°09′W, 350 m, *Feuillet 2926* (MO). GUYANA. **East Berbice:** margins of Berbice River, S of New Dageraad, 06°00′N, 57°43′W, *Maas et al. 5573* (U). **Mazaruni:** Upper Mazaruni River Basin, Akapai, 470 m, *Tillett & Tillett 45685* (MO). SURINAME. **Nickerie:** right bank of Corantijn River, N of Kaboerie Cr., *Heyde 449* (MO). **Para:** Jodensavanne-Mapanekreek, Suriname River, *Kramer & Hekking 7450* (U). **Saramacca:** Fluv. Saramacca, Mt. Janbasigado, *Pulle 170* (U). **Wanika:** between Tawajari-Weg and de Crane-Weg, W of Lelydorp in old sec. wood on white sand, *Heyde 596* (MO). VENEZUELA. **Bolívar:** Río Paragua, hasta 12 vueltas arriba de la boca del Río Tonoro, 06°03′N, 63°47′W, 175 m, *Stergios 10320* (MO). **Delta Amacuro:** E of Río Grande, E of El Palmar, *Gentry & Berry 14938* (MO). **Mérida:** Marcano Berti, *Luis 199* (MO, VEN).

When intact tendrils are not present on a specimen, the short bracts and bracteoles of *Roentgenia sordida* make it particularly difficult to distinguish from the sympatric *Cydista aequinoctialis* (L.) Miers, although the latter can usually be distinguished by dark glandular fields (when dried) in the axils of the secondary veins beneath; these glandular fields were not observed in *Roentgenia*. Gentry (1978: 279) suggested that the racemose-paniculate inflorescence and overall leaf appearance of *Cydista lilacina* A. H. Gentry "links" the genera *Cydista*, *Roentgenia*, and *Clytostoma*. However, *C. lilacina* is distinct from other *Cydista* species in its curved bud apices and 4-seriate ovules (Hauk, 1997), and these two features serve to distinguish *C. lilacina* from *R. sordida*. The "bromeliad-like," persistent pseudostipules and echinate fruit of *Clytostoma* are distinct from the foliaceous, caducous pseudostipules and rough (but plane) fruit of *R. sordida*. *Potamoganos microcalyx* (G. Mey.) Sandw. is partially sympatric with *R. sordida* and has trifid tendrils, but *P. microcalyx* differs from *R. sordida* in having a nectariferous disk.

Potamoganos Sandw., Recueil Trav. Bot. Néerl. 34: 220–221. 1937. TYPE: *Potamoganos microcalyx* (G. Mey.) Sandw.

Lianas; stems woody with 4 phloem arms in cross section, branchlets terete to subtetragonal with interpetiolar glandular fields present and distal to the node, the transverse interpetiolar ridges not evident, the younger branchlets striate and glabrate to lepidote; pseudostipules caducous, subfoliaceous, triangular, eglandular, lepidote. *Leaves* opposite, estipulate, petiolate, 2- or 3-foliolate with the terminal leaflet often modified into a trifid tendril; petioles terete, glabrate; petiolules terete to sulcate, glabrate to lepidote; leaflets entire, marginally plane; axils of secondary veins lacking glandular fields. *Inflorescences* elongate, axillary racemes, unbranched, several-flowered; rachis and peduncles flattened to nearly terete, glabrate to lepidote, bracteate, the bracts minute, caducous, lacking circular glandular fields, glandular-lepidote; pedicels flattened, glabrate to lepidote; bracteoles minute, caducous, eglandular, glandular-lepidote. *Flowers* ovoid in bud; calyx cupular-campanulate, eglandular, lepidote, the calyx margin intact, the apex truncate except for five minute teeth; corolla zygomorphic, campanulate-funnelform, lavender to magenta, glabrate to sparsely lepidote, with an inner ring of pubescence proximal to the insertion of the stamens; corolla lobes 5 (2 upper and 3 lower), short-orbicular, the inner surface glabrate, the outer surface glabrate to lepidote; stamens 5, fertile stamens didynamous with the fifth stamen modified into a staminode, all adnate to the corolla; fertile anthers with two spreading thecae, included, glabrous; nectariferous disk present; ovary cylindrical, densely lepidote, the ovules 4-seriate in each locule; stigma included, bipartite, the divisions laterally flattened. *Fruit* not seen.

1. Potamoganos microcalyx (G. Mey.) Sandw., Recueil Trav. Bot. Néerl. 34: 220–221. 1937. *Bignonia microcalyx* G. Mey., Prim. Fl. Esseq. 211. 1818. TYPE: Guyana, *Meyer s.n.* (holotype, GOET not seen), not seen by Gentry. Figure 2.

Bignonia microcalyx var. *acuminata* Miq., in Flora 25(2): 427. 1842. TYPE: Suriname, (holotype?, U not seen).

Anemopaegma cupulatum Bureau & K. Schum., in Mart., Fl. Bras. 8 pt. 2, fasc. 121: 146. 1897. TYPE: Suriname, without exact locality, *Wullschlaegel 1034* (BR not seen).

Lianas; branchlets drying brown to red-brown, striate, glabrate, lenticels not evident; pseudostipules triangular, 1 × 1 mm, eglandular, lepidote. *Leaves* 15–25 cm long, once-pinnate, bifoliolate with a terminal leaflet often modified into a trifid tendril; petioles 3.5–11.0 cm long, glabrate to puberulent or lepidote; petiolules 0.5–3.5 cm long, glabrate to lep-

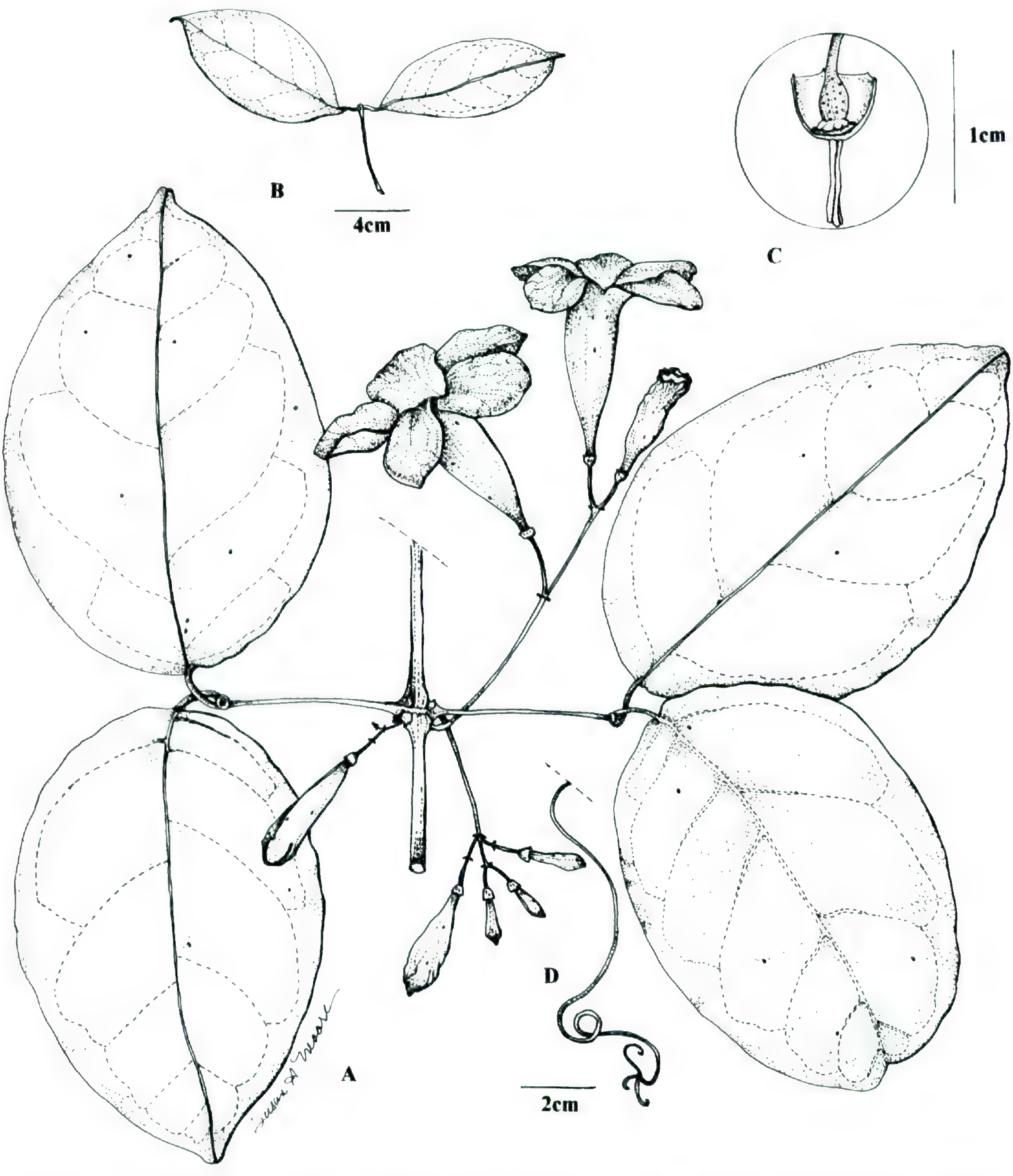

Figure 2. *Potamoganos microcalyx*.—A. Inflorescence and leaves, after *Miller & Hauk 9418*.—B. Young leaflets, after *Miller & Hauk 9418*.—C. Detail showing calyx, ovary, and nectariferous disk, after *Miller & Hauk 9418*.—D. Tendril, after *Miller & Hauk 9418*.

idote; leaflets 6.5–13 × 4.0–8.5 cm, elliptic to suborbicular, plane, chartaceous, glabrate with a few minute glands scattered over the surface, apically acute to obtuse, basally broadly acute to rounded, with 4 to 5 principal vein pairs, marginally plane. *Inflorescences* to 20 cm long; bracts linear, 1.0 × 0.5 mm; bracteoles linear, 0.5–1.0 × 0.5 mm; flowers ovoid in bud; calyx 3–5 × 5–6 mm, glabrate to sparsely lepidote; corolla exserted 35–55 mm beyond the level of the calyx lip (40–60 mm total length), 2.5–3.0 mm wide at the calyx lip, the corolla tube lepidote inwardly and glabrate outwardly; corolla lobes 18 × 15 mm; fertile stamens 12 or 18 mm long, inserted ca. 5 mm beyond the corolla tube base, the staminode 3 mm long, inserted 3 mm beyond the corolla tube base; disk 1 mm tall; ovary 2–3 mm long; style 15–20 mm long. *Fruit* not seen. *Figures:* Gentry (1983, fig. 37; 1997, fig. 407).

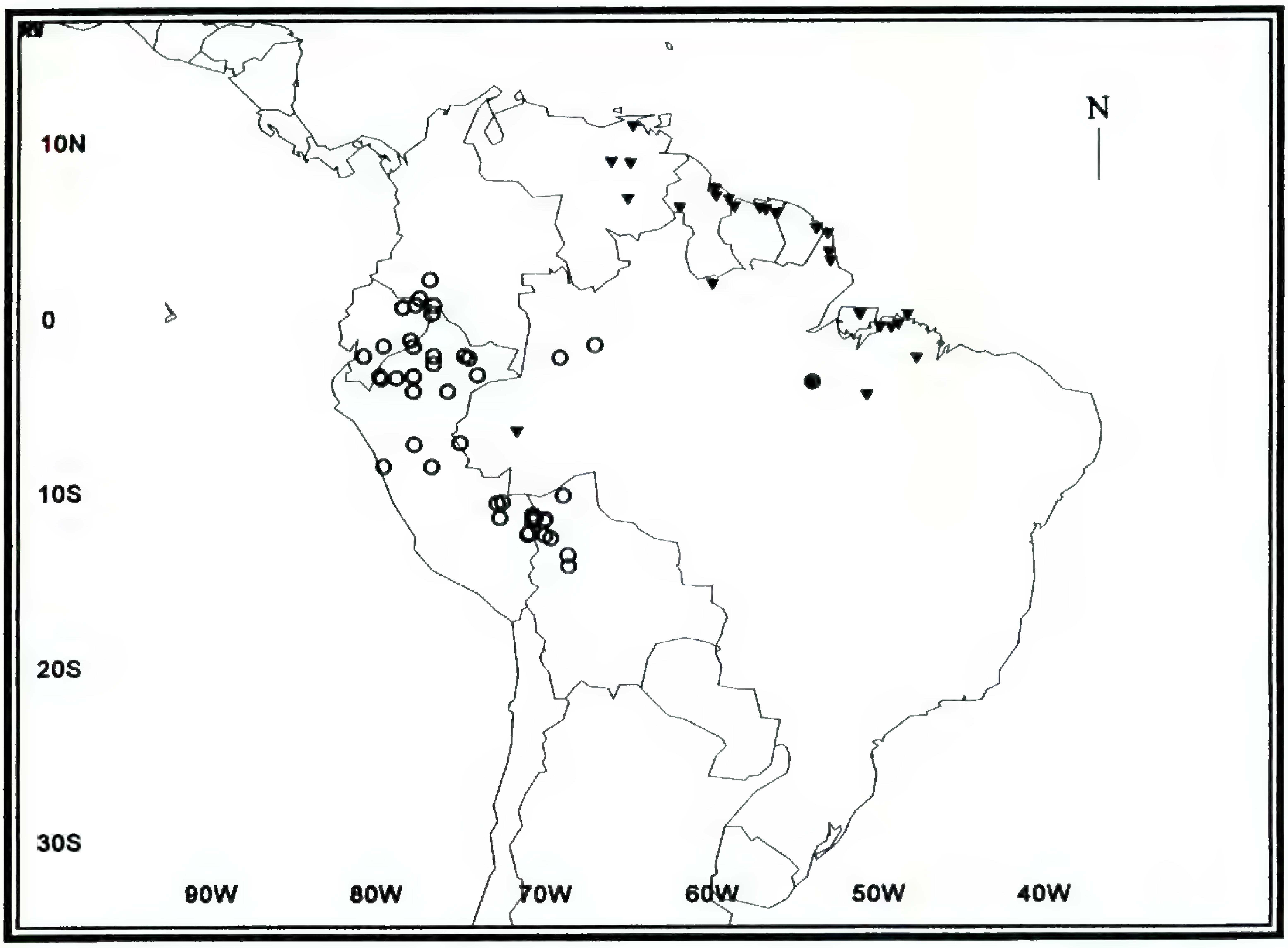

Figure 3. Geographic distribution of collections of *Roentgenia bracteomana* (circles) and *R. sordida* (triangles) in South America.

Distribution, elevation, and habitat. Known from south-central Venezuela, Guyana, Suriname, and portions of northern Brazil (Fig. 4). Collections are reported from 0 to 300 m in mixed lowland forest, often on lateritic soils.

Phenology. Four flowering collections were examined: February (1), April (1), May (1), and October (1). No fruiting collections were seen or have been documented.

Additional specimens. BRAZIL. **Amapa:** without exact locality, 02°03′N, 50°48′W, *Ducke 1973* (MG). **Amazonas:** Boa Vista Road, 64 km N of Manaus, 02°40′S, 60°08′W, *Lowe 4190* (MO). GUYANA. Vicinity of Kartabo Station, junction of Mazaruni and Cuyuni Rivers, 06°30′N, 58°40′W, *Graham 307* (CM). **Rupununi:** foothills of NW Kanuku Mts., near Moco-Moco village, 03°20′N, 59°35′W, 100 m, *Maas & Westra 3906* (MO). **Essequibo:** Malali, Demerara River, 05°50′N, 58°15′W, *de la Cruz 2726* (CM, US); Arawau Trail, 23 mi. from Linden, 06°00′N, 58°15′W, 20 m, *Grewal 16* (U). SURINAME. **Voltzberg:** without exact locality, *Pulle 307* (U). **Saramacca:** Coppename River, 3 km below base camp, 05°30′N, 55°50′W, *Florschutz & Maas 2734* (U). **Sipaliwini:** Mamadam, 04°40′N, 55°40′W, *Florschutz & Florschutz 1155* (U); Montibus Bakhuisinter fluv. Kabalebo & Coppename Sinistera, Kabalebo River 1–5 km below airstrip, 03°50′N, 56°50′W, *Florschutz & Maas 2340* (U); area of Kabalebo Dam project, 04°10′N, 57°10′W, *Heyde & Lindeman 192* (MO); vicinity of Blanche Marie falls on the Nickerie River, 04°45′N, 56°52′W, 60 m, *Miller & Hauk 9418* (BBS, MO); Fluv. Saramacca, prope Mt. Janbasigado, 04°20′N, 55°30′W, *Pulle 415* (MO, U). VENEZUELA. **Amazonas:** 23 km NE of Puerto Ayacucho, 05°51′N, 67°25′W, 90 m, *Davidse & Huber 15362* (MO); Río Orinoco below San Fernando de Atabapo, Cano Morocoto, 1 hour below San Fernando, 04°10′N, 67°42′W, *Gentry et al. 10947* (MO); Río Cuao, Río Orinoco, 04°55′N, 67°40′W, 125 m, *Maguire & Politi 28436* (NY, US); Cerro Huachamacari, Río Cunucunuma, 03°48′N, 65°46′W, 400 m, *Maguire et al. 29973* (VEN).

The shape and color of the *Cydista*-type corollas of *P. microcalyx* are easily confused with those of the sympatric *Cydista aequinoctialis* (L.) Miers and *C. lilacina* A. H. Gentry. However, the inflorescence axes of *P. microcalyx* are longer and more flattened than either *Cydista* species, and the calyx is shorter and more cupular. The nectariferous disk and trifid tendrils of *P. microcalyx* should readily distinguish it from all *Cydista* species. Gentry (1997) noted that the leaves of *Potamoganos microcalyx* are similar to those of *Distictella* Kuntze and *Ceratophytum* Pitt., but that the inflorescences and flowers more closely resemble *Mansoa* A. DC.

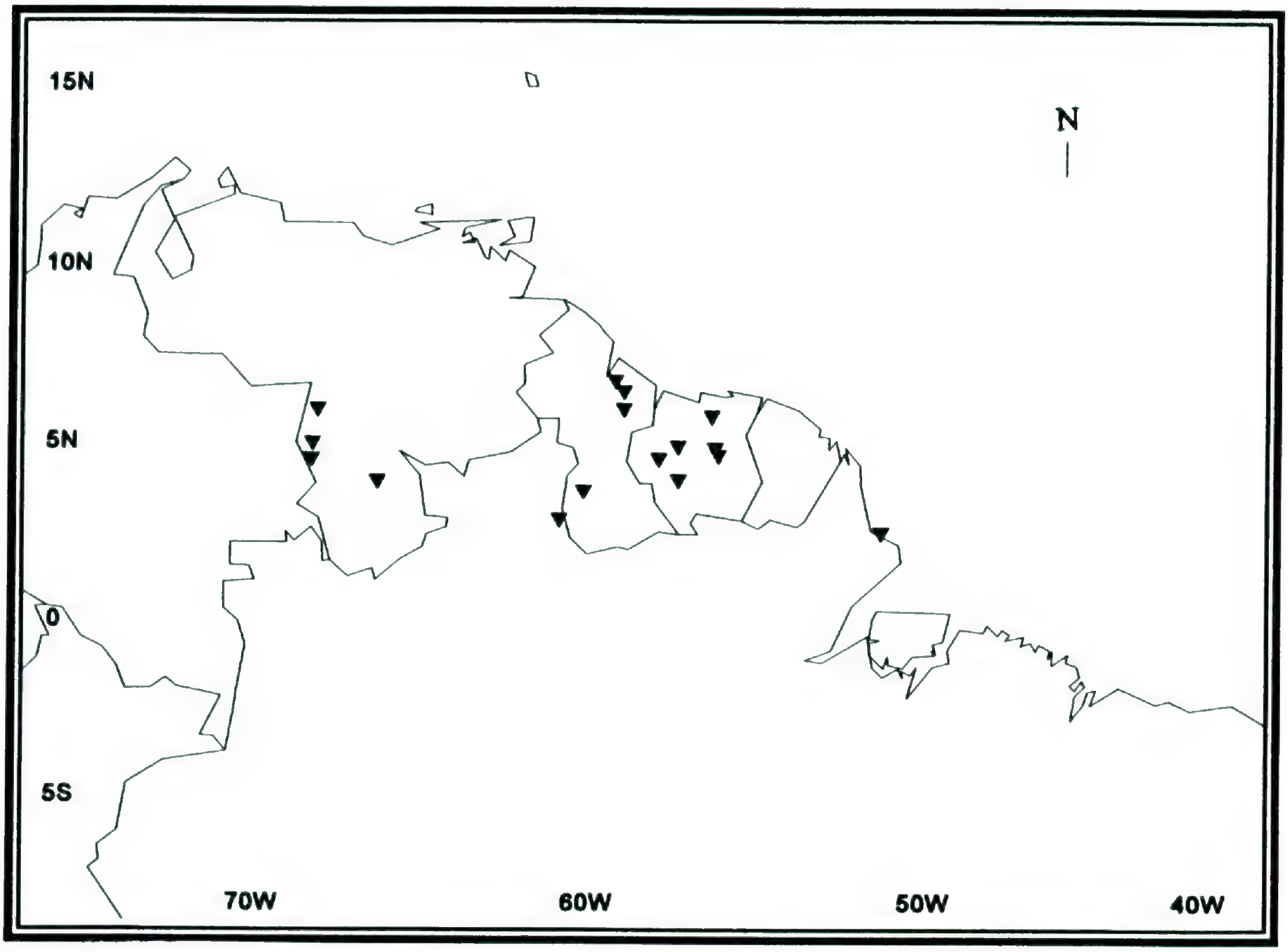

Figure 4. Geographic distribution of collections of *Potamoganos* in northern South America.

and *Roentgenia*. Like *Potamoganos*, *Roentgenia* has a trifid tendril, but the nectariferous disk is absent, and the bracts and bracteoles of *P. microcalyx* are not trisect, as is found in *Roentgenia*.

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Appendix 1

Index to Numbered Exsiccatae

Collections are listed alphabetically by the principal author, followed by collection number, and a boldface number (1–3) that indicates the species collected. All specimens entered into TROPICOS were assumed to have

been examined by A. H. Gentry. Specimens examined by the author were limited to duplicates housed at MO, and are indicated by a "!". The coding of the species numbers is as follows: *Roentgenia bracteomana* = **1**, *Roentgenia sordida* = **2**, *Potamoganos microcalyx* = **3**.

Archer, W. A. 8095 **2**; Aronson, J. 1039! **1**; Ayala, F. et al. 3927! **1**.

Balée, W. L. 1958 **1**, 1968 **2**, 3517! **2**; Beck, H. T. et al. 416! **2**; Benoist, R. 897! **2**; Black, G. A. 47–819 **2**; Boi, P. MG8796 **2**; Brandbyge, J. & Asanza, E. 30067! **1**; Burnham, R. J. 1563! **1**.

Cazalet, P. C. & Pennington 7558! **1**; Cerón, C. E. & Ayala, J. 9469! **1**; Cremers, G. 4502! **2**; Croat, T. B. 21259! **1**; Cruz, J. S. de la 2726! **3**; Cuatrecasas, J. 10834 **1**.

Davidse, G. & O. Huber 15362! **3**; Díaz S., C. & J. Ruiz 924! **1**; Díaz S., C. et al. 1297! **1**; dos Santos, G. et al. 73! **2**, 85! **2**, 118! **2**, 133! **2**; Ducke 1973 **3**.

Emmons, L. 21! **1**, 49! **1**, 133! **1**.

Feuillet, C. 2926! **2**; Florschutz, P. & Florschutz 1155 **3**; Florschutz, P. & Maas 2340, 2734 **3**; Foster, R. B. 9388! **1**; Foster, R. B. & B. d'Achille 12004! **1**; Froes, R. L. 31509 **2**.

Gentry, A. H. 13077! **2**, 49133! **2**; Gentry, A. H. & P. Berry 14938! **2**, 14970! **2**; Gentry, A. H. & Díaz, C. 58505! **1**; Gentry, A. H. & L. Emmons 39592! **1**; Gentry, A. H. & S. Estensoro 70344! **1**; Gentry, A. H. & R. Foster 70842! **1**; Gentry, A. H. & N. Jaramillo 57542! **1**, 57683! **1**; Gentry, A. H. & P. Núñez 59559 **1**, 69435! **1**, 69559! **1**; Gentry, A. H. & J. Revilla 16336! **1**; Gentry, A. H. & K. Young 31820! **1**; Gentry, A. H. et al. 9169! **1**, 10947! **3**; 21798! **1**, 22064! **1**, 23649! **1**, 25849! **1**, 26787! **1**, 27287! **1**, 45772! **1**, 46076! **1**, 68670! **1**, 76904! **1**, 76941! **1**; Graham, E. 307 **3**; Grewal 16 **3**; Grández, C. & A. Chiquispama 938! **1**.

Heyde, N. M. 449! **2**, 596! **2**; Heyde, N. M. & J. C. Lindeman 192! **3**; Holm-Nielsen, L. et al. 21432 **1**; Huashikat, V. 2158! **1**.

Jaramillo, J. & F. Coello 4433! **1**.

Killip, E. P. 37704 **2**; Killip, E. P. & A. C. Smith 28169 **1**; Klug, G. 2043! **1**, 2176! **1**; Kramer & Hekking 7450 **2**; Krukoff, B. A. 8623! **2**, 8847 **2**; Kujikat 357 **1**.

Lindeman, J. C. 4050 **2**, 5008 **2**, 5197 **2**; Linder, D. H. 80 **2**; Lowe, J. 410! **3**; Londoño, C. et al. 124! **3**; Lugo, H. 2557! **1**, 2570! **1**, 2703! **1**.

Maas, P. J. M. & L. Y. Th. Westra 3906! **3**; Maas, P. J. et al. 5573 **2**; Maguire, B. & L. Politi 28436 **3**; Maguire, B. et al. 29973 **3**; Marcano-Berti, L. 199! **2**; McDaniel, S. & B. Marcos 11000! **1**; Mexía, Y. 6320! **1**; Miller, J. S. & W. D. Hauk 9418! **3**; Mori, S. et al. 17251! **2**; Mori, S. & R. Souza 17263! **2**.

Neill, D. et al. 6283! **1**; Núñez, P. 6149! **1**, 11852! **1**, 12210! **1**; Núñez, P. & M. Timaná 12149A! **1**.

Oldeman, R. A. 2303 **2**; Øllgaard, B. et al. 34586! **1**.

Palacios, W. et al. 8717! **1**; Phillips, O. et al. 329! **1**; Pinkus 1! **2**; Pires, J. M. & N. T. Silva 11042 **2**, 11044 **2**; Plowman, T. & Schunke 7503! **1**; Prance, G. T. et al. 30271! **2**, 30306! **2**; Pulle, A. 170 **2**, 307 **3**, 415! **3**, 462pp **2**, 495 **2**.

Rue, de la 40 **2**.

Sandwith, N. Y. 577 **2**; Schulz, J. 8371 **2**; Schunke V., J. 4608! **1**, 5696! **1**, 11788 **1**; Seibert, R. J. 2146! **1**; Siqueires, R. MG8824 **2**; Smith, A. C. 2847! **2**; Smith, D. N. et al. 13258! **1**, 14115! **1**; Smith, S. F. & Shuhler 400! **1**; Smith, S. F. et al. 620! **1**, 1454! **1**; Steege, H. et al. 357! **3**; Stergios, B. 10320! **2**; Stergios, B. & L. Delgado 12998! **2**.

Tessmann, G. 3245 **1**; Tillett, S. S. & Tillett 45685! **2**; Timaná, M. & P. Smith 1426! **1**; Timaná, M. & O. Phillips 1881! **1**.

Ule, E. 5497 **1**.

Woytkowski, F. 5637! **1**.

Young, K. 25! **1**; Young, H. J. & D. A. Stratton 3! **1**.

APPENDIX 2

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MOLECULAR DATA INDICATE COMPLEX INTRA- AND INTERCONTINENTAL DIFFERENTIATION OF AMERICAN *DRABA* (BRASSICACEAE)[1]

Marcus Koch[2] *and Ihsan A. Al-Shehbaz*[3]

Abstract

The genus *Draba* includes about 350 species distributed primarily in the Northern Hemisphere, with some 80 species in South and Central America. Although species of *Draba* are well described morphologically, the existing sectional classification is highly controversial. American taxa exhibit enormous morphological differences even among species of the same section. We tested the hypothesis that variation accumulated during migration and differentiation of American *Draba*. The present phylogenetic study is based on analyses of the ITS (internal transcribed spacer) regions of the nuclear ribosomal DNA and the chloroplast *trn*L-intron and spacer sequences from 72 American *Draba* taxa and 6 European *Draba* species. Results suggest that some intrageneric groupings correspond primarily to phytogeography, and that only to a small degree do these findings agree with previous sectional classification. Differences between ITS- and *trn*L-derived phylogenies suggest extensive genetic contact may have existed between some of the groups or sections and that this disjunction between European and American *Draba* is demonstrated by ITS sequence data. Plastid DNA sequences suggest that the "European" plastome types may be more widely distributed among the American *Draba* species, perhaps through multiple transmissions of Eurasian chloroplast types into American *Draba*. Additional systematic analysis demonstrates that the genus *Erophila* has to be integrated into *Draba*. Analysis on the tribal level reveals the entire *Draba* complex to be close to European *Arabis* and *Aubrieta*. The data provide additional support for previous assumptions that the existing tribal classifications of the Brassicaceae are mostly artificial and that the segregation of *Draba* and *Arabis* into separate tribes or subtribes does not accurately reflect their phylogenetic relationship.

Key words: Brassicaceae, *Draba*, *Erophila*, molecular systematics, reticulate evolution.

The wide occurrence of polyploidy in vascular plants reflects its importance to plant speciation. The origin of polyploids and the mechanisms behind the establishment of newly evolved populations and taxa are among the challenging questions in plant sciences (Ramsey & Schemske, 1998; Thompson & Lumaret, 1992; Petit et al., 1999; Soltis & Soltis, 1999). New combinations of favorable genes may be more easily stabilized in polyploid taxa, and the permanent coexistence of favorable traits and characters from different parental lines may be effectively preserved as fixed heterozygosity (Soltis & Soltis, 1993). These speciation processes are integral to the genesis and maintenance of plant biodiversity. Recent studies of the overall genome structure of hybrid and polyploid taxa provide new insights about the dynamic nature of complete genomes either analyzed on the basis of artificial hybrids or by comparative mapping (Rieseberg et al., 1999; Rieseberg & Linder, 1999; Lagercrantz, 1998; Kowalski et al., 1994). In their comparative genome analysis of some Brassicaceae, Acarkan et al. (2000) showed that structural rearrangements occurred with a significantly higher frequency in polyploid *Brassica* L. than in diploid *Arabidopsis thaliana* (L.) Heynh. or *Capsella rubella* Reuter. This suggests that at the structural level a more dynamic nature of the genome might be sustained in polyploid taxa than in diploid ones, and this might be a remarkable source for new genetic variation upon which selective pressures can then act.

Draba L. is the largest genus of the Brassicaceae and includes ca. 350 species, or about 10% of the family total (Al-Shehbaz, 1987). The genus is distributed primarily in the Northern Hemisphere, especially in the subarctic to arctic regions and alpine or mountainous portions of the temperate regions. Nearly half of the taxa are found in the

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New World and about 80 species are distributed in Central and South America (Al-Shehbaz, 1987). Schulz (1927, 1936) divided the genus into 17 sections (Table 1), but Fernald (1934) criticized this artificial sectional classification largely on its misleading and impractical keys. Further, Tolmachev (1939) totally ignored Schulz's sections and recognized 29 series for the 91 species occurring in the former Soviet Union. No subsequent botanists have attempted to subdivide *Draba* into infrageneric taxa. For European *Draba*, most authors have followed Walters (1964) who correctly used section *Draba* instead of Schulz's section *Leucodraba* DC., because section *Draba* includes the generic type.

A few case studies have investigated the phylogenetic relationships among some Arctic Scandinavian (Brochmann et al., 1992a–d, 1993) and alpine European (Widmer & Baltisberger, 1999a, b) species of *Draba*. Some general aspects of these studies have been previously outlined (Brochmann, 1992) and can be summarized as: (1) allopolyploidy is common, with a polyphyletic and polytopic origin for some taxa; (2) gene flow across different ploidy levels is possible and probably occurs in natural populations; (3) complex evolutionary phylogenetic networks have been demonstrated for section *Draba* and some species of section *Chrysodraba*; (4) repeated migration and colonization contribute to complex distribution patterns; and (5) not unexpectedly, items 1 through 4 are substantiated by molecular studies with complex patterns of intra- and interspecific variation observed (Brochmann et al., 1992a–d; Widmer & Baltisberger, 1999a, 1999b). Support also exists at morphological, cytological, and ecological levels (Brochmann, 1993; Brochmann et al., 1993).

Isozyme electrophoresis and DNA analysis of the nuclear and plastid genome have greatly increased the possibility of detecting and distinguishing allo- and autopolyploids, to trace paternal and maternal genome lineages, and to document hybridization, introgression, and reticulate evolution within polyploid complexes. Several polyploid complexes in the Brassicaceae have been characterized, including those of the genera *Microthlaspi* F. K. Meyer (Koch et al., 1998b; Koch & Hurka, 1999), *Draba* (Brochmann & Elven, 1992; Brochmann, 1993; Brochmann et al., 1992a–d, 1993), *Cochlearia* L. (Koch et al., 1998a, 1999b), *Yinshania* Y. C. Ma & Y. Z. Zhao (Koch & Al-Shehbaz, 2000), *Cardamine* L. (Franzke et al., 1998; Urbanska et al., 1997), *Biscutella* L. (König, 1998), *Brassica* L. and related genera (Anderson & Warwick, 1999), and *Nasturtium* R. Br. (Bleeker et al., 2000).

In order to gain a better understanding of the phylogenetic relationships within a large polyploid complex, we examined the sequence variation from the internal transcribed spacer regions (ITS1 and ITS2) of nrDNA for American species of *Draba* (Baldwin et al., 1995; Campbell et al., 1995), the cp *trn*L intron (Taberlet et al., 1991; Gielly & Taberlet, 1994; van Ham et al., 1994; Koch & Al-Shehbaz, 2000), and the cp *trn*L-*trn*F spacer (Taberlet et al., 1991). The derived molecular phylogenies were then compared with traditional concepts based on morphological data.

Materials and Methods

Plant material, DNA extraction, PCR-amplification, and sequencing

Leaf material for DNA extraction was obtained from herbarium specimens (Table 1). DNA was isolated from 25–50 mg of dried leaf material using the NucleonPhytoPure Kit (Amersham Lifescience) following the instructions of the supplier. DNA was stored in 10 mM Tris-EDTA buffer pH 8.0 at −20°C.

Double-stranded DNA of the complete ITS region, including the 5.8 S rDNA region, was amplified by 35 cycles of symmetric PCR using ITS primers initially designed by White et al. (1990) and modified by Mummenhoff et al. (1997a) for ITS4. The PCR profile used to amplify the ITS region followed the following profile: a hot start with 5 min. at 94°C, and 35 cycles of amplification (1 min. 94°C, 45 sec. 38°C, 45 sec. 72°C), final elongation step for 10 min. at 72°C, and storage at 4°C. The 18F primer (5′-GGAAGGAGAAGTCGTAACAAGG-3′) is located at the 3′-end of the 18 S rDNA gene and primer 25R (5′-TCCTCCGCTTATTGATATGC-3′) is located at the 5′-end of the 25 S rDNA. PCR products were purified using the Boehringer PCR product purification kit (Roche Molecular Biochemicals). PCR products spanned the entire ITS1, 5.8 S rDNA, and ITS2 region and were cycle-sequenced directly without cloning using the Taq DyeDeoxy Terminator Cycle Sequencing Kit (ABI Applied Biosystems, Inc.) and the 18F and 25R primers. Products of the cycle sequencing reactions were run on an ABI 377XL automated sequencer.

The *trn*L (UAA) intron was amplified and sequenced by using the universal primers "c" (B49317, 5′-CGAAATCGGTAGACGCTACG-3′) located at the 3′-end of the *trn*L(UAA)5′-exon and "d" (A49855, 5′-GGGGATAGAGGGACTTGAAC-3′) located at the 5′-end of the *trn*L(UAA)3′-exon (Taberlet et al., 1991). The PCR profile used to amplify the *trn*L intron followed Koch and Al-Sheh-

Table 1. Accession data of the material under study. Additional explanation is indicated on the table itself.

Taxon	Country, collector (herbarium acronym)	Acc. no.	Sectional classification according to Schulz (1927); see Table 2	ITS1, 5.8S rDNA, and ITS2	*trn*L intron	*trn*L spacer
Cusickiella douglasii (A. Gray) Rollins	U.S.A., *Tiehm & Williams 7998* (MO)	78		AF146515	AF146959	AF146962
C. quadricostata (Rollins) Rollins	U.S.A., *Tiehm & Williams 7929* (MO)	77		AF146514	AF146960	AF146961
Draba aizoides L.	Germany, *Neuffer s.n.* (OSBU #3818)	103	*Aizopsis*	AF146511	AF146957	AF146964
D. aizoides L.	Switzerland, Widmer & Baltisberger, 1999b	107	*Aizopsis*	AF120721	AF120727	
D. aizoides L.	Switzerland, Widmer & Baltisberger, 1999b	108	*Aizopsis*		AF120730	
D. aizoides L.	Switzerland, Widmer & Baltisberger, 1999b	109	*Aizopsis*		AF120731	
D. aizoides L.	Austria, *Neuffer s.n.* (OSBU#5199)	104	*Aizopsis*	AF146512	AF146958	AF146963
D. alyssoides HBK	Ecuador, *Sklenar & Kostechova 162* (MO)	23		AF146456	AF146904	AF147017
D. araboides Wedd.	Peru, *Tovar 959* (US)	84	*Tomostima*	AF146505	AF146952	AF146969
D. aureola	U.S.A., *Hurka 3189* (OSBU)	101	*Phyllodraba*	AF146509	AF146956	AF146965
D. barclayana Al-Shehbaz	Colombia, *Barclay & Juajibioy 7398* (GH)	11		AF146449	AF146898	AF147023
D. bellardii S. F. Blake	Venezuela, *Ruiz-Terán & López-Figueiras 10469* (MO)	7	*Chamaegongyle*	AF146446		
D. boyacana Al-Shehbaz	Colombia, *Grubb et al. 303* (K)	79		AF146500	AF146947	AF146974
D. carinthiaca Hoppe	Switzerland, Widmer & Baltisberger, 1999b	105	*Leucodraba*		AF120737	
D. chionophila S. F. Blake	Venezuela, *Berry 4273* (MO)	8	*Chamaegongyle*	AF146447	AF146897	AF147024
D. confertifolia Turcz.	Ecuador, *Spruce 5796* (MO)	35	*Calodraba*	AF146463	AF146910	AF147011
D. crassifolia Graham	U.S.A., *Stein et al. 1881* (MO)	59	*Drabella*	AF146482	AF146930	AF146991
D. cruciata Payson	U.S.A., *Sharsmith 3338* (MO)	60	*Chrysodraba*	AF146483	AF146931	AF146990
D. cryophila Cuatrec.	Colombia, *Cuatrecasas & Romero 24611* (US)	5		AF146444	AF146895	AF147026
D. cryptantha Hook. f.	Peru, *Smith et al. 10673* (MO)	28	*Tylodraba*	AF146457		
D. cuatrecasana Rangel & Santana	Colombia, *Cleef 7668* (US)	1		AF146441	AF146892	AF147029
D. cuneifolia Nutt. ex Torr. & A. Gray	U.S.A., *Rollins & Rollins 8747* (MO)	61	*Tomostima*	AF146484	AF146932	AF146989
D. densifolia Nutt.	U.S.A., *Hurka 2837* (OSBU)	102	*Chrysodraba*	AF146510		
D. densifolia Nutt. ex Torr. & A. Gray	U.S.A., *Rollins & Rollins 78228* (MO)	62	*Chrysodraba*	AF146485	AF146933	AF146988
D. depressa Hook. f.	Ecuador, *Sklenar & Kostechova 1269* (MO)	30	*Tylodraba*	AF146458	AF146905	AF147016
D. dubia Suter	Switzerland, Widmer & Baltisberger, 1999b	114	*Leucodraba*	AF120722	AF120738	
D. extensa Wedd.	Ecuador, *Asplund 8595* (US)	85	*Tylodraba*	AF146506	AF146953	AF146968
D. farsetioides Linden & Planch.	Venezuela, *RuizTerán & López-Figueiras 1064* (MO)	31	*Calodraba*	AF146459	AF146906	AF147015
D. funckiana Linden & Planch.	Venezuela, *Gines 4706* (US)	32	*Chamaegongyle*	AF146460	AF146907	AF147014
D. funckiana Linden & Planch.	Venezuela, *Gines 4706* (US)	87	*Chamaegongyle*	AF146508	AF146955	AF146966
D. funiculosa Hook. f.	Argentina, *Pisano & Garaventa 2736* (MO)	33	*Linodraba*	AF146461	AF146908	AF147013

Table 1. Continued.

Taxon	Country, collector (herbarium acronym)	Acc. no.	Sectional classification according to Schulz (1927); see Table 2	ITS1, 5.8S rDNA, and ITS2	*trn*L intron	*trn*L spacer
D. gilliesii Hook. & Arn.	Chile, *Taylor & Taylor 108848* (MO)	34	*Calodraba*	AF146462	AF146909	AF147012
D. glabella Pursh	U.S.A., *Hodgdon 8922* (MO)	63	*Leucodraba*	AF146486	AF146934	AF146987
D. hallii Hook. f.	Ecuador, *Humbles 6330* (MO)	36	*Calodraba*	AF146464	AF146911	AF147010
D. hammenii Cuatrec & Cleef	Colombia, *Cleef 9070* (US)	2		AF164442	AF146893	AF147028
D. helleriana Greene	Mexico, *Sharp 45753* (MO)	54	*Phyllodraba*	AF146478	AF146925	AF146996
D. hemsleyana O. E. Schulz	Ecuador, *Ramsay & Merrow-Smith 24* (MO)	83	*Calodraba*	AF146504	AF146951	AF146970
D. hidalgensis Calderón	Mexico, *Rzedowski 26804* (MO)	55		AF146479	AF146926	AF146995
D. hitchcockii Rollins	U.S.A., *Rollins et al. 83263* (MO)	64		AF146487	AF146935	AF146986
D. incerta Payson	U.S.A., *Rollins et al. 83323* (MO)	65	*Leucodraba*	AF146488	AF146936	AF146985
D. jaegeri Munz & Johnson	U.S.A., *Clokey 7949* (MO)	66		AF146489	AF146937	AF146984
D. jorullensis HBK	Mexico, *Weaver 2126* (MO)	56	*Adenodraba*		AF146927	AF146994
D. jorullensis HBK	Mexico, *Breedlove 26720* (MO)	57	*Adenodraba*	AF146480	AF146928	AF146993
D. ladina Br.-Bl.	Switzerland, Widmer & Baltisberger, 1999b	115	*Leucodraba*	AF120723	AF120740	
D. ladina Br.-Bl.	Switzerland, Widmer & Baltisberger, 1999b	116	*Leucobrada*	AF120724		
D. lapaziana Al-Shehbaz	Bolivia, *Solomon 13219* (MO)	21		AF146455	AF146903	AF147018
D. lindenii (Hook.) Planch.	Venezuela, *Berry 4029* (MO)	38	*Doliostylis*	AF146465	AF146912	AF147009
D. litamo Uribe	Colombia, *Grupp et al. 833* (MO)	39		AF146466		
D. macleanii Hook. f.	Peru, *Smith et al. 10674* (MO)	40	*Rhabdodraba*	AF146467	AF146913	AF147008
D. magellanica Lam.	Argentina, *Pisano & Garaventa 2717* (MO)	41	*Leucodraba (Holarges)*		AF146914	AF147007
D. matthioloides O. E. Schulz	Peru, *Holt 191* (K)	82	*Calodraba*	AF146503	AF146950	AF146971
D. mogollonica O. E. Schulz	Peru, *Holt 191* (K)	67	*Phyllodraba*	AF146490	AF146938	AF146983
D. nivicola Rose	Mexico, *Zola et al. 72* (MO)	58	*Adenodraba*	AF146481	AF146929	AF146992
D. oligosperma Hook.	U.S.A., *Rollins & Rollins 79233* (MO)	68	*Chrysodraba*	AF146491	AF146939	AF146982
D. paysonii Macbride	U.S.A., *Rollins et al. 83306* (MO)	71	*Chrysodraba*	AF146494	AF146941	AF146980
D. pennell-hazenii O. E. Schulz	Colombia, *Forero et al. 3634* (MO)	3	*Chamaegongyle*	AF146443	AF146894	AF147027
D. peruviana (DC.) O. E. Schulz	Peru, *Macbride 4440* (MO)	43	*Calodraba*	AF146468	AF146915	AF147006
D. pickerengii A. Gray	Peru, *Solomon 3329* (MO)	44	*Rhabdodraba*	AF146469	AF146916	AF147005
D. platycarpa Torr. & A. Gray	U.S.A., *Correll & Little 27171* (MO)	69	*Tomostima*	AF146492	AF146940	AF146981
D. pseudocheiranthoides Al-Shehbaz	Colombia, *Barclay & Juajibioy 6733* (MO)	12		AF146450		
D. pterosperma Payson	U.S.A., *Hitchcock & Martin 5317* (MO)	70	*Chrysodraba*	AF146493		
D. pulvinata Turcz. subsp. *pulvinata*	Venezuela, *Ewan 16951* (K)	80	*Doliostylis*	AF146501	AF146948	AF146973

Table 1. Continued.

Taxon	Country, collector (herbarium acronym)	Acc. no.	Sectional classification according to Schulz (1927); see Table 2	ITS1, 5.8S rDNA, and ITS2	*trn*L intron	*trn*L spacer
D. pulvinata Turcz. subsp. *berryi* Al-Shehbaz	Venezuela, *Berry 4030* (MO)	18	*Doliostylis*	AF146454	AF146902	AF147019
D. pusilla F. Philippi	Chile, *Ruthsatz 7026* (MO)	45	*Drabella*	AF146470	AF146917	AF147004
D. pycnophylla Turcz.	Ecuador, *Luteyn et al. 8910* (MO)	46	*Calodraba*	AF146471	AF146918	AF147003
D. ramosissima Desvaux	U.S.A., *Kral 49698* (MO)	76	*Phyllodraba*	AF146499	AF146946	AF146975
D. reptans (Lam.) Fernald	U.S.A., *Muehlenbach 3498* (MO)	72	*Tomostima*	AF146495	AF146942	AF146979
D. ritacuvana Al-Shehbaz	Colombia, *Barclay & Juajibioy 7323-A* (GH)	13		AF146451	AF146899	AF147022
D. rositae Santana & Rangel	Colombia, *Rangel 3105* (GH)	14		AF146452	AF146900	AF147021
D. schusteri O. E. Schulz	Peru, *Weberbauer 6033* (GH)	15	*Rhabdodraba*	AF146453	AF146901	AF147020
D. scopulorum Wedd.	Bolivia, *Solomon 5023* (MO)	47	*Rhabdodraba*	AF146472	AF146919	AF147002
D. sericea Santana & Rangel	Colombia, *Cleef 5261* (MO)	48		AF146473	AF146920	AF147001
D. solitaria O. E. Schulz	Peru, *Weberbauer 7235* (US)	6	*Calodraba*	AF146445	AF146896	AF147025
D. soratensis Wedd.	Bolivia, *Solomon 13136* (MO)	49	*Rhabdodraba*	AF146474	AF146921	AF147000
D. splendens Gilg	Ecuador, *Ollgard & Balslev* 10080 (MO)	50	*Calodraba*	AF146475	AF146922	AF146999
D. spruceana Wedd.	Ecuador, *Spruce 5766* (GH)	9	*Adenodraba*	AF146448		
D. standleyi Macbride & Payson	U.S.A., *Goodman & Hitchcock 1168* (MO)	74		AF146497	AF146944	AF146977
D. streptocarpa A. Gray	U.S.A., *Park 86* (MO)	73	*Phyllodraba*	AF146496	AF146943	AF146978
D. stylaris Koch	Widmer & Baltisberger, 1999b	106	*Leucodraba*		AF120736	
D. stylosa Turcz.	Ecuador, *Jameson 150* (K)	81		AF146502	AF146949	AF146972
D. subumbellata Rollins & Price	U.S.A., *Morefield & Ross 4712* (MO)	75		AF146498	AF146945	AF146976
D. tomentosa Clairv.	Switzerland, Widmer & Baltisberger, 1999b	112	*Leucodraba*	AF120725	AF120741	
D. tomentosa Clairv.	Switzerland, Widmer & Baltisberger, 1999b	113	*Leucodraba*	AF120726		
D. tucumanensis O. E. Schulz	Argentina, *Jörgensen 1574* (MO)	51		AF146476	AF146923	AF146998
D. violacea HBK	Ecuador, *Jameson s.n.* (US#534920)	86	*Calodraba*	AF146507	AF146954	AF146967
D. wurdackii Al-Shehbaz	Peru, *Sánchez Vega 4149* (MO)	52		AF146477	AF146924	AF146997
Erophila spathulata A. F. Láng	Austria, *Englisch 2655/98*	111		AF377952		
E. verna (L.) Chev.	Austria, *Englisch 2711/98*	110		AF377951		

baz (2000): a hot start with 5 min. at 94°C, and 35 cycles of amplification (1 min. 94°C, 45 sec. 50°C, 45 sec. 72°C), a final elongation step for 10 min. at 72°C, and storage at 4°C. PCR products were purified and cycle-sequenced as described for ITS analysis using the amplification primer c and d. The *trn*L(UAA)-*trn*F(GAA) intergenic spacer was amplified using the following primers: the universal primer "e" designed by Taberlet et al. (1991) (5′-GGTTCAAGTCCCTCTATCCC-3′) and a newly designed primer *trn*F-IGS-rev (5′-AGGATTTTCAGTCCTCTGCTC-3′). Amplification, purification, and sequencing were performed as described for the *trn*L intron.

DATA ANALYSIS

Outgroup selection. The genus *Draba* has been variously placed into the tribes Alysseae or Drabeae (Hayek, 1911; Schulz, 1936; Janchen, 1942; Al-Shehbaz, 1987). However, as pointed out by Al-Shehbaz (1987), the Alysseae are a poorly defined tribe with about 40 genera (15 monotypic) and some 650 species distributed primarily in the Irano-Turanian and Mediterranean regions. Recent molecular studies (Price et al., 1994; Koch et al., 1999a, 2000, 1999b) clearly indicate that nearly all tribal subdivisions of the Brassicaceae are highly artificial. Therefore, we used the aligned ITS data set from Koch et al. (1999a) in which tribal structures were analyzed, and taxa from the tribes Lepidieae, Sisymbrieae, and Arabideae were considered to infer relative phylogenetic position of taxa under investigation. We added sequence data from *Erophila verna* (L.) Chev., *D. araboides* Wedd., *D. aizoides* L., and *Cusickiella quadricostata* (Rollins) Rollins (accession nos. 110, 84, 103, and 77, respectively, Table 1) to the alignment described by Koch et al. (1999a). We included *C. quadricostata* because it was originally described in *Draba*, and only recently it and *D. douglassii* A. Gray were transferred to the newly established *Cusickiella* Rollins (Rollins, 1988). Data analysis, distance and parsimony methods, were performed as described in Koch et al. (1999a) to get comparable results to this analysis. The results were used to choose an appropriate outgroup. Our analysis herein demonstrated that the European *Arabis* L. and *Aubrieta deltoidea* (L.) DC. are closer to *Draba* than *Cusickiella* is. Therefore, European *Arabis* (*A. alpina*, *A. bryoides*, *A. pumila*, *A. blepharophylla*) and *Aubrieta deltoidea* were selected as outgroups for the further ITS study of *Draba*. *Cusickiella* was excluded from all further analysis.

ITS data. DNA sequences were aligned by hand. In addition to sequences from American *Draba*, we included 6 ITS sequences from European *Draba* from Widmer and Baltisberger (1999a, Table 1) and 6 sequences from *Arabis/Aubrieta* serving as outgroups (Koch et al., 1999a), resulting in a total matrix of 80 ITS sequences. Distance analyses were performed with Kimura-2-parameter distances using PHYLIP software package version 3.57c (Felsenstein, 1995). The neighbor-joining algorithm was used for tree construction. Bootstrap analysis (Felsenstein, 1985) was performed using 1000 replicates. For all analyses gaps were coded as missing characters. The parsimony analysis began with a subset of taxa comprising representatives from all putative clades included in the overall analysis. This analysis was performed to demonstrate relative branch length and to estimate additional confidence parameters. The second data matrix used was identical in alignment to the first data matrix. Parsimony analysis was performed with unordered Fitch parsimony using PAUP* 4.0b2 (Swofford, 1999). The branch-and-bound algorithm was used to find maximally parsimonious trees. Bootstrap analysis (Felsenstein, 1985) was performed using 1000 replicates with the bootstrap search algorithm. Decay analysis (Bremer, 1988) was performed in addition to the bootstrap approach, in order to assess the confidence that could be placed in the monophyly of clades. Decay indices (DI) were estimated according to Baum et al. (1994). For all parsimony analyses gaps were coded as missing characters.

trnL intron and spacer data. DNA sequences were aligned by hand using the boundaries of coding regions as anchor points with which to begin the alignments. We included 8 *trn*L intron and spacer sequences from European *Draba* (Widmer & Baltisberger, 1999b, Table 1) and 67 American *Draba* for a total of 75 *trn*L sequences. *Draba cuneifolia* (acc. no. 61), *D. platycarpa* (acc. no. 69), *D. reptans* (acc. no. 72), and *D. araboides* (acc. no. 84), which are only distantly related to remaining ingroup taxa (results from the ITS analysis), were used as outgroups. The ancestral position of these four taxa with respect to the remaining *Draba* analyzed herein was also confirmed by an analysis using *trn*L intron and *trn*L-*trn*F spacer regions from *Arabis alpina* L. and *Aubrieta deltoidea* L. (GenBank accession numbers AY034180 and AY034181, respectively). Distance analyses were performed for the total data set as described for the ITS data. In order to obtain a relative support for branching patterns of representatives from all putative clades, a subset of *Draba* taxa was investigated with Fitch parsimony as described for ITS analysis. For this analysis gaps were coded as additional binary (0/1)

characters. All gaps differing in length and position were coded as separate binary characters. The distribution of gaps and its coding can be viewed at http://homepage.boku.ac.at/koch/.

Missing data. Amplification failed to yield ITS data for *Draba magellanica* (acc. no. 41) and *D. jorullensis* (acc. no. 56), and *trn*L intron and spacer data was missing for *D. bellardii* (acc. no. 7), *D. spruceana* (acc. no. 9), *D. pseudocheiranthoides* (acc. no. 12), *D. cryptantha* (acc. no. 28), *D. litamo* (acc. no. 39), *D. pterosperma* (acc. no. 70), and *D. densifolia* (acc. no. 102). For *Draba carinthiaca* (acc. no. 105) and *D. stylaris* (acc. no. 106) only *trn*L intron and spacer data were available, and for the two *Erophila* species no plastidic data were available. Data matrices are available upon request or can be viewed at http://homepage.boku.ac.at/koch/.

Results

Outgroup selection and tribal relationships

Our reexamination and analysis combining the ITS data matrix (a sampling of 36 ITS sequences from species across Arabideae, but excluding *Draba*) from Koch et al. (1999a) with sequences added from *Erophila verna*, *Draba araboides*, *D. aizoides*, and *Cusickiella quadricostata* (in capital letters, Fig. 1) resulted in trees identical in topology to the phylogenetic hypothesis presented in that paper. The data matrix of 603 bp contained 342 invariable characters. From the remaining 261 variable nucleotide positions 163 sites were potentially informative. Fitch parsimony analysis resulted in 12 most parsimonious trees with a length of 612 steps, a consistency index (CI) of 48.9% (autapomorphies excluded), and a retention index (RI) of 71.8%. The strict consensus tree (not shown) out of these 12 most parsimonious trees is identical (except for *Erophila verna*, *Draba aizoides* and *D. araboides*, and *Cusickiella quadricostata* that are added herein) to the previously published phylogenetic network (Koch et al., 1999a). The distance tree is identical to that presented by Koch et al. (1999a) (Fig. 1). *Draba* is closely related to the European *Arabis* L. and *Aubrieta* Adans., and it is positioned within an "Arabideae core group" (Fig. 1). The genus *Cusickiella*, which is endemic to the western United States, was resolved with North American *Halimolobus* Tausch and North American *Arabis*. As shown by Koch et al. (1999a), the North American *Arabis*, excluding the *A. blepharophylla* Hook. & Arn. group and a few other species, are better treated in the genus *Boechera* A. Löve & D. Löve (Löve & Löve, 1975). For subsequent ITS analysis of all *Draba* taxa, European *Arabis* and *Aubrieta* were used as outgroups, and *Cusickiella* has been excluded from all subsequent analysis.

ITS data

The analysis of phylogenetic relationships among ingroup taxa comprises 80 ITS sequences from *Draba* and *Erophila* of which 74 sequences are novel. Six ITS sequences from *Arabis* and *Aubrieta* were used to root phylogenetic trees as outlined above. The total length of the aligned data matrix is 626 bp. From 283 bp within the ITS1 region, 109 sites were variable (including 37 autapomorphic changes); from 166 bp within the 5.8 S rDNA, 11 sites were variable (all autapomorphic changes); and from 177 bp within the ITS2 region, 20 sites were variable (all autapomorphic changes). This results in a total of 68 potentially informative sites. Uncorrected pairwise sequence distances ranged up to 10% within outgroup taxa (59 nucleotide positions), up to 9.3% within ingroup taxa (57 nucleotide positions), and up to 12.3% among the whole data set. Argentinian *Draba funiculosa* Hook. f. (acc. no. 33) was excluded from these calculations because of an unusual ITS type that differed markedly from the remaining *Draba* taxa (13.1 to 16.6% sequence divergence or 82 to 104 nucleotide positions). However, in the phylogenetic analysis *D. funiculosa* clustered among European *Draba* (Fig. 2). The whole alignment required 44 gap positions of 1 nucleotide in length, and 2 gap positions required 4 (*Arabis alpina*, *A. blepharophylla*) and 14 (*A. alpina* L., *Aubrieta deltoidea*) base pairs, respectively. Identical ITS sequences were detected in *D. lindenii* and *D. pulvinata* subsp. *pulvinata* (acc. nos. 38 and 80, respectively) and in *D. sericea* (acc. no. 48), *D. splendens* (acc. no. 50), *D. hemsleyana* (acc. no. 83), and *D. extensa* (acc. no. 85). The results of the distance analysis are shown in Figure 2. Six major clades (I–VI as indicated on Fig. 2) could be distinguished among the genus *Draba* with relatively robust support for clades I–III (Fig. 2).

We also indicated Schulz's (1927) sectional classification (Table 2) in Roman numerals in the phylogenetic ITS tree (Fig. 2).

Fitch parsimony analysis with a subset of *Draba* taxa from all major groups recognized in the overall analysis resulted in 12 most parsimonious trees (MPTs) 208 steps in length, CI of 70% (autapomorphies excluded), and RI of 69.9%. The results of the bootstrap and decay analysis are added to the strict consensus tree shown in Figure 3.

The overall analysis (Fig. 2), as well as the anal-

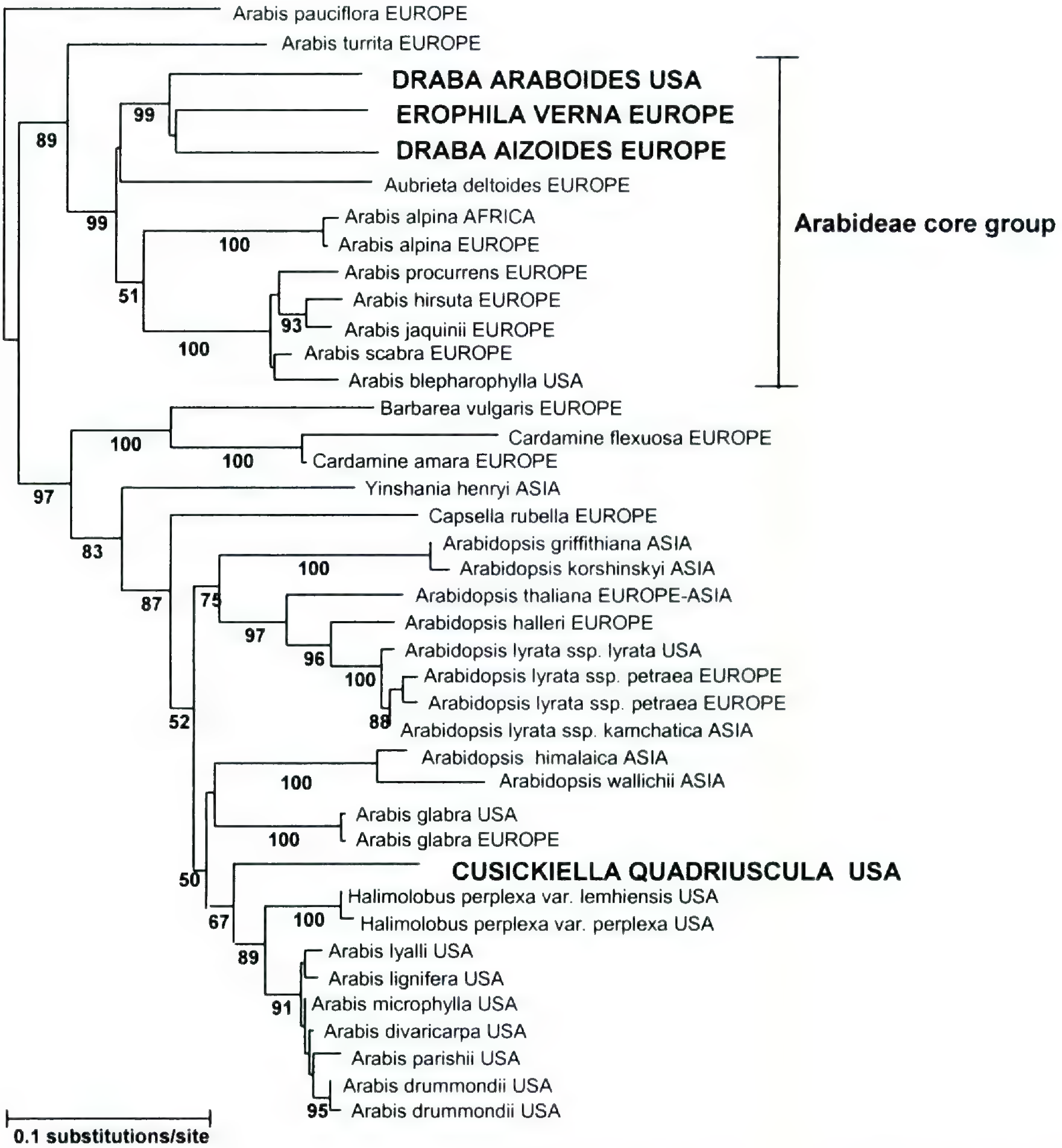

Figure 1. Neighbor-joining distance tree based on ITS sequence data to demonstrate the systematic relationships of *Draba* to other cruciferous taxa. Sequences from four taxa analyzed in this study (shown in capital letters) were added to a previous analysis of tribe Arabideae (Koch et al., 1999a). *Draba* and *Erophila* were integrated into an "Arabideae core group" previously recognized by Koch et al. (1999a). Distributional area is indicated. For *Arabis glabra* (L.) Bernh. herein we used the taxonomically more appropriate synonym *Turritis glabra* L. Bootstrap support is given below the branches from 1000 replicates.

ysis of a subset of taxa (Fig. 3), recognized the same six major ITS clades among European and American *Draba*, including the two accessions of *Erophila*. European *Draba* are confined to clade III together with European *Erophila* (Figs. 2 and 3); this clade is characterized by long internal genetic distances separating European taxa from the remaining American *Draba*. The American species of *Draba* are found in all remaining clades I, II, IV, V, and VI.

The most basal clade, clade I, combines sequences from mostly North American *Draba* taxa (*D. cuneifolia*, acc. no. 61; *D. platycarpa*, acc. no. 69; *D. reptans*, acc. no. 72), but also one accession from Peru (*D. araboides*, acc. no. 84). Clades I–III are well supported by bootstrap values of 100%, 88%, and 93%, respectively. In contrast, clades IV, V, and VI (combining the majority of taxa) are only weakly supported by bootstrap analysis (Fig. 2). However, all clades were recognized in the parsimony analysis with a subset of taxa from all six clades. The only exception is *D. scopulorum* (acc.

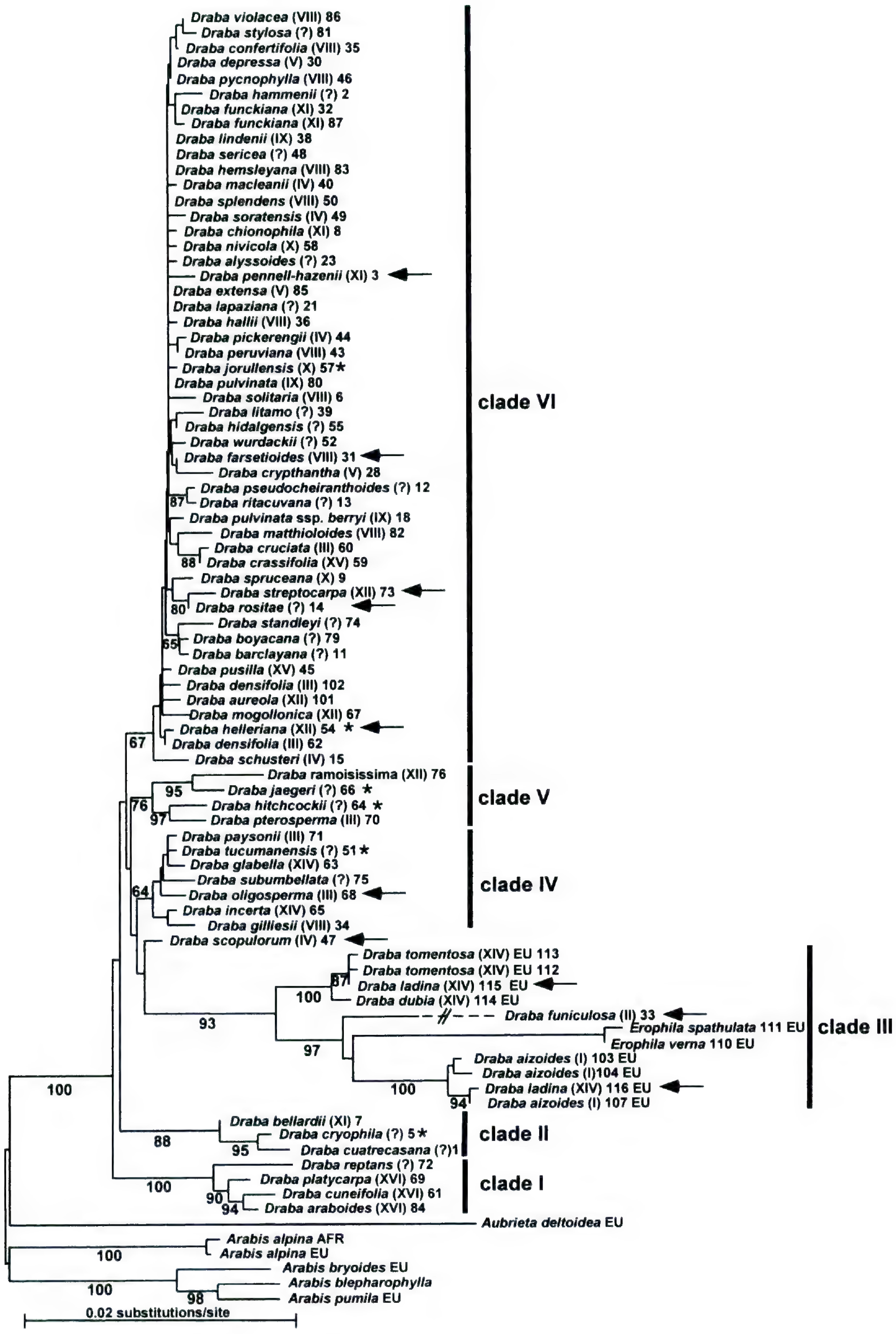
Draba violacea (VIII) 86
Draba stylosa (?) 81
Draba confertifolia (VIII) 35
Draba depressa (V) 30
Draba pycnophylla (VIII) 46
Draba hammenii (?) 2
Draba funckiana (XI) 32
Draba funckiana (XI) 87
Draba lindenii (IX) 38
Draba sericea (?) 48
Draba hemsleyana (VIII) 83
Draba macleanii (IV) 40
Draba splendens (VIII) 50
Draba soratensis (IV) 49
Draba chionophila (XI) 8
Draba nivicola (X) 58
Draba alyssoides (?) 23
Draba pennell-hazenii (XI) 3
Draba extensa (V) 85
Draba lapaziana (?) 21
Draba hallii (VIII) 36
Draba pickerengii (IV) 44
Draba peruviana (VIII) 43
Draba jorullensis (X) 57*
Draba pulvinata (IX) 80
Draba solitaria (VIII) 6
Draba litamo (?) 39
Draba hidalgensis (?) 55
Draba wurdackii (?) 52
Draba farsetioides (VIII) 31
Draba crypthantha (V) 28
Draba pseudocheiranthoides (?) 12
87
Draba ritacuvana (?) 13
Draba pulvinata ssp. berryi (IX) 18
Draba matthioloides (VIII) 82
Draba cruciata (III) 60
88
Draba crassifolia (XV) 59
Draba spruceana (X) 9
Draba streptocarpa (XII) 73
80
Draba rositae (?) 14
Draba standleyi (?) 74
65
Draba boyacana (?) 79
Draba barclayana (?) 11
Draba pusilla (XV) 45
Draba densifolia (III) 102
Draba aureola (XII) 101
Draba mogollonica (XII) 67
Draba helleriana (XII) 54 *
67
Draba densifolia (III) 62
Draba schusteri (IV) 15
clade VI
Draba ramoisissima (XII) 76
95
Draba jaegeri (?) 66 *
76
Draba hitchcockii (?) 64 *
97
Draba pterosperma (III) 70
clade V
Draba paysonii (III) 71
Draba tucumanensis (?) 51*
Draba glabella (XIV) 63
Draba subumbellata (?) 75
64
Draba oligosperma (III) 68
Draba incerta (XIV) 65
Draba gilliesii (VIII) 34
clade IV
Draba scopulorum (IV) 47
Draba tomentosa (XIV) EU 113
Draba tomentosa (XIV) EU 112
87
Draba ladina (XIV) 115 EU
100
Draba dubia (XIV) 114 EU
93
Draba funiculosa (II) 33
Erophila spathulata 111 EU
97
Erophila verna 110 EU
Draba aizoides (I) 103 EU
Draba aizoides (I)104 EU
100
Draba ladina (XIV) 116 EU
94
Draba aizoides (I) 107 EU
clade III
100
Draba bellardii (XI) 7
Draba cryophila (?) 5*
88
95
Draba cuatrecasana (?)1
clade II
Draba reptans (?) 72
Draba platycarpa (XVI) 69
100
90
Draba cuneifolia (XVI) 61
94
Draba araboides (XVI) 84
clade I
Aubrieta deltoidea EU
Arabis alpina AFR
100
Arabis alpina EU
Arabis bryoides EU
100
Arabis blepharophylla
98
Arabis pumila EU
0.02 substitutions/site

Table 2. Sectional classification system according to Schulz (1927). Roman numerals correspond to those used in parentheses in Figure 2.

Sectional classification according to Schulz (1927)	Number of species and distribution
I. *Aizopsis* DC.	28 spp., Mediterranean and rest of Europe
II. *Linodraba* O. E. Schulz	1 sp., South American (Falkland Islands and Patagonia)
III. *Chrysodraba* DC.	57 spp., Asia and North America
IV. *Rhabdodraba* O. E. Schulz	10 spp., South America
V. *Tylodraba* O. E. Schulz	8 spp., South America (Ecuador and Peru)
VI. *Acrodraba* O. E. Schulz	1 sp., NW Africa (Morocco)
VII. *Helicodraba* O. E. Schulz	2 spp., NW Africa (Morocco)
VIII. *Cladodraba* O. E. Schulz	14 spp., South America (Colombia south into Patagonia)
IX. *Dolichostylis* (Turcz.) O.E. Schulz	3 spp., South America (Venezuela)
X. *Adenodraba* O. E. Schulz	9 spp., Central America (Mexico and Guatemala) and South America (Colombia, Ecuador, and Bolivia)
XI. *Chamaegongyle* O. E. Schulz	6 spp., South America (Colombia and Venezuela)
XII. *Phyllodraba* O. E. Schulz	29 spp., North America, E. Asia, and Himalayas
XIII. *Nesodraba* Greene	1 sp., North America
XIV. *Leucodraba* DC.	59 spp., Europe, Asia, North America, and South America (2 spp.)
XV. *Drabella* DC.	23 spp., Asia, North America, and South America (2 spp.)
XVI. *Tomostima* (Raf.) O. E. Schulz	6 spp., North America and South America (2 spp.)
XVII. *Abdra* (Greene) O. E. Schulz	1 sp., North America

no. 47). This species was positioned between clades IV and III by distance analysis (Fig. 2) with higher sequence similarity to taxa from clade IV, but parsimony analysis positioned it in clade IV with high confidence (Fig. 3). We obtained no significant phylogenetic structuring among these six major clades, and the trees remained unresolved in this respect.

TRNL DATA

We considered 76 sequences of which 69 are novel reports herein. In total we considered 72 different taxa. The alignment of the *trn*L intron is 382 bp in length and contained 6 bp of the first exon of the *trn*L(UAA) gene at the 5′-end and 30 bp of the second exon at its 3′-end. The alignment of the *trn*L-F-intergenic spacer region is 404 bp in length and contained 5 bp of the second exon of the *trn*L(UAA) gene at its 5′-end and 15 bp of the *trn*F gene at the 3′-end. Both alignments were combined to a final alignment 786 bp in length consisting of the entire *trn*L intron as well as the second exon of the *trn*L gene and the complete *trn*L-F-intergenic spacer. A region of six base pairs between the intron and the spacer that showed no variation among *Draba* accessions sequenced by Widmer and Baltisberger (1999b) is missing. The whole data matrix is interspersed with 24 gaps (7 within the *trn*L intron, including 4 autapomorphies, and 17 within the spacer region, including 8 autapomorphies, respectively). Within the *trn*L intron 47 variable nucleotide positions were detected (including 20 autapomorphies); within the *trn*L-F spacer 52 out of 87 variable nucleotide positions were uninformative. The distance tree is shown in Figure 4 with support indicated by bootstrap greater than 50%.

Fitch parsimony analysis with a subset of taxa similar to the ITS analysis resulted in 182 MPTs with 112 steps in length, CI of 72%, and RI of 79%. This subset comprises the same set of taxa used for ITS analysis with additional *Draba rositae* (acc. no. 14), because this taxon has been separated from other *Draba* taxa by a relatively high bootstrap support of 63% (Fig. 4). Significant results of the bootstrap and decay analysis are shown along

←

Figure 2. Neighbor-joining distance tree of ITS sequence data. Bootstrap support is given from 1000 replicates. Arrows indicate positions of taxa that differ from the plastid analysis (see Fig. 4). Asterisks mark accessions that were used for triplet comparisons of ITS types to investigate concerted evolution (for details refer to text). Branch length of *Draba funiculosa* (acc. no. 33, clade III) has not been drawn to scale (refer to text). Taxonomic accession numbers correspond to those in Table 1. In parentheses the sectional position according to Schulz (1927) is given. Taxa that were not recognized by Schulz (1927) are marked with "?". ITS sequences of outgroup taxa from *Arabis* and *Aubrieta* have been published previously by Koch et al. (1999a). European *Draba* are indictaed by "EU."

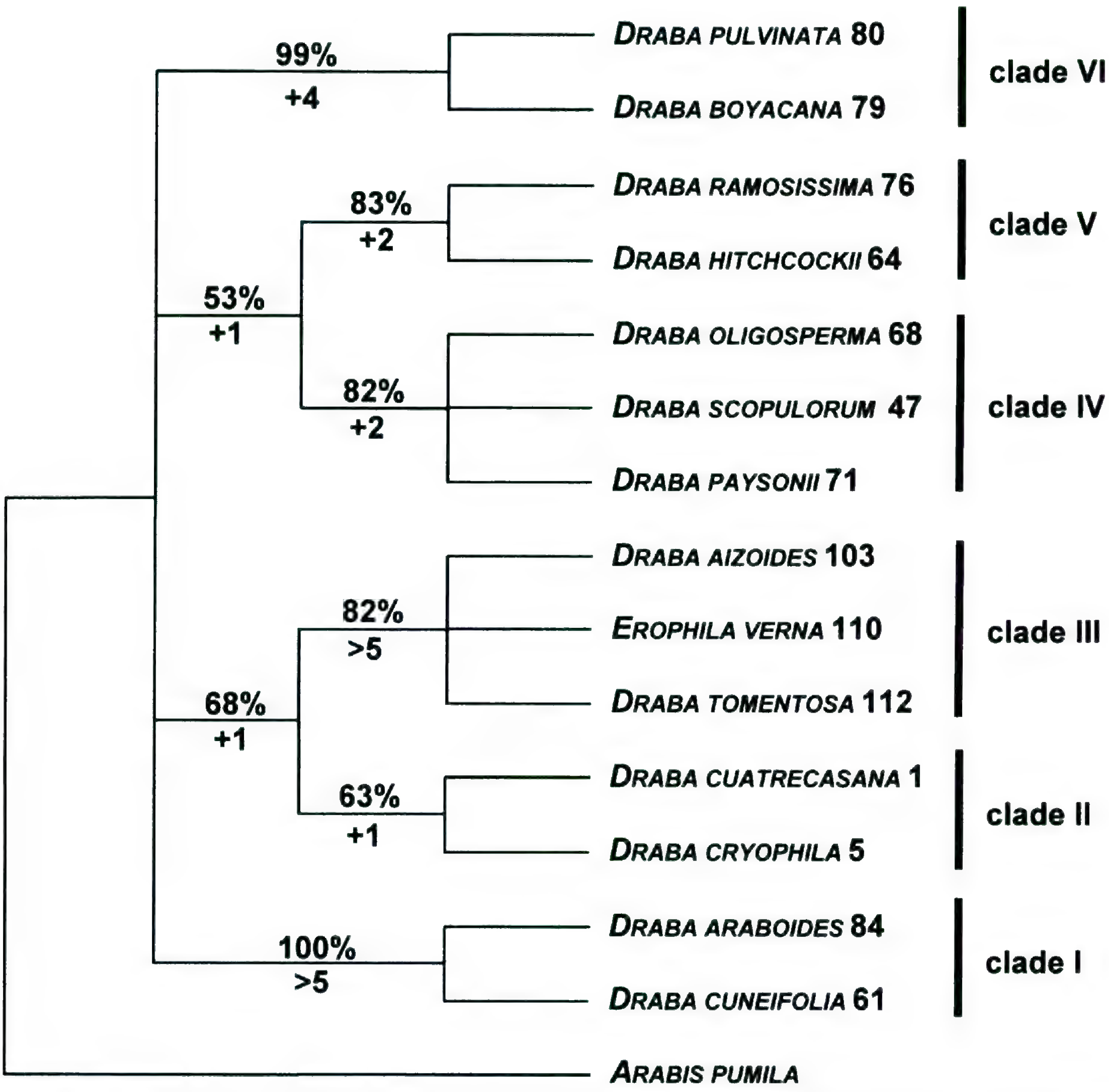

Figure 3. Strict consensus tree from Fitch parsimony using a subset of ITS sequences. Bootstrap support from 1000 replicates is seen above branches; decay values are indicated below branches. Accession numbers following taxa correspond to Table 1. Clades I–V correspond to ITS clades I–V from Figure 2.

branches in the strict consensus tree (Fig. 5). The results of this analysis are congruent with the findings of the overall distance analysis (Fig. 4). Five major clades could be distinguished (clades A–E, Figs. 4 and 5) with bootstrap support greater than 50%. There is no support to combine *D. oligosperma* (acc. no. 68) and *D. scopulorum* (acc. no. 47) to any of these clades. However, *D. oligosperma* is more closely related to cp genome types C and D (Figs. 4 and 5) as revealed from distance and parsimony analysis.

The occurrence of these particular cp genome types according to their geographic origin is summarized in Table 3.

The more inclusive distance analysis (Fig. 4) recognized five major clades among *Draba*, with *D. cuneifolia* (acc. no. 61), *D. platycarpa* (acc. no. 69), *D. reptans* (acc. no. 72), and *D. araboides* (acc. no. 84) in clade A only distantly related to the remaining clades. Plastome types from European *Draba* were found mostly in clades B and D, but one additional plastome type from *Draba aizoides* (acc. no. 108) (Widmer & Baltisberger, 1999b) showed an intermediate position between clades E and C/D. In the present analysis, three plastome types of *D. aizoides* from Widmer and Baltisberger (1999b) were included and all three were diverse. *Draba aizoides* herein investigated from Germany (acc. no. 103) is more closely related to *D. aizoides* (acc. no. 107 from Widmer & Baltisberger, 1999b); it assorts

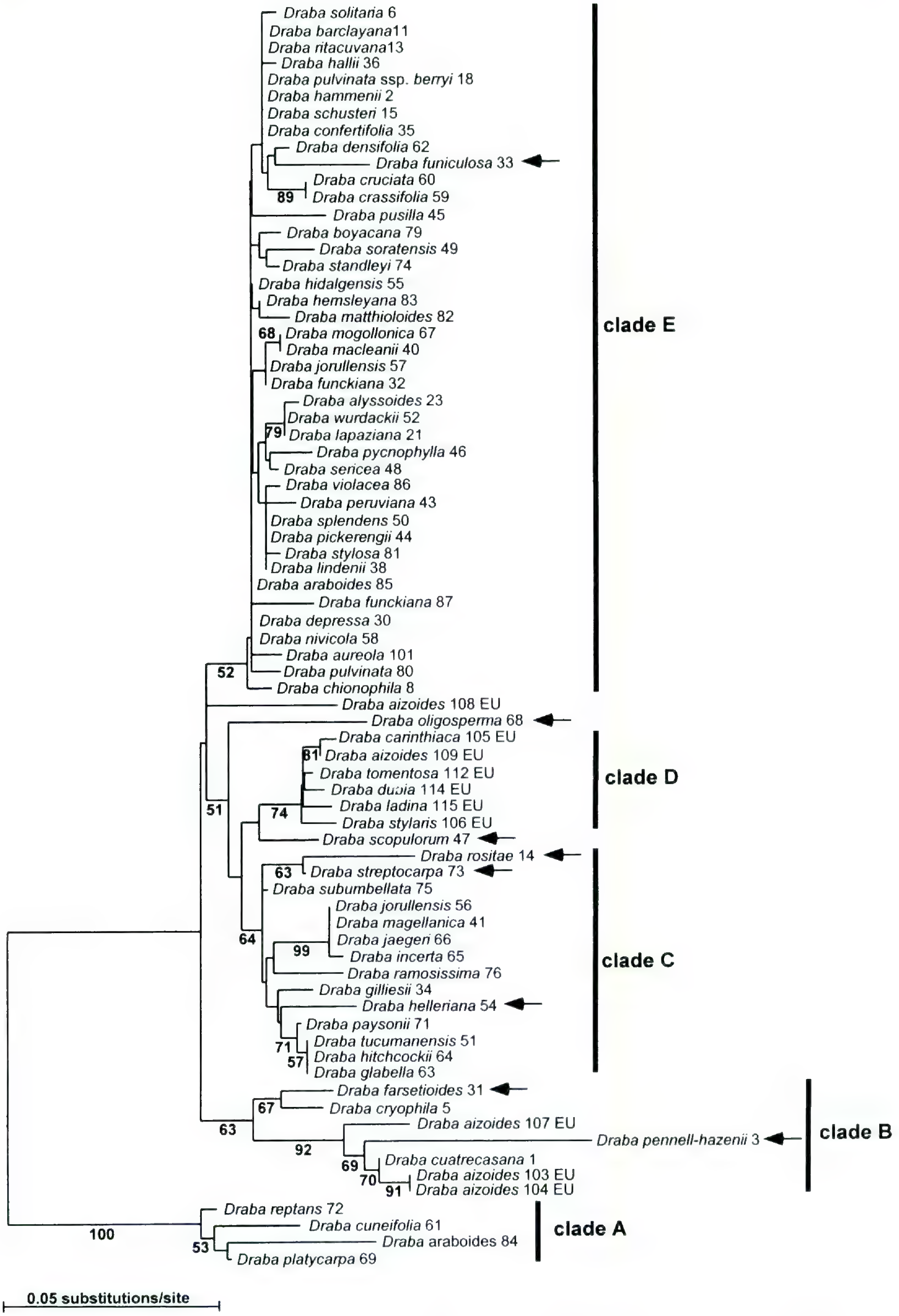

Figure 4. Neighbor-joining distance tree of *trn*L sequence data. Bootstrap support is given from 1000 replicates. Arrows indicate positions of taxa that differ from the ITS analysis (see Fig. 2). Accession numbers of taxa correspond to Table 1. European *Draba* are indictaed by "EU."

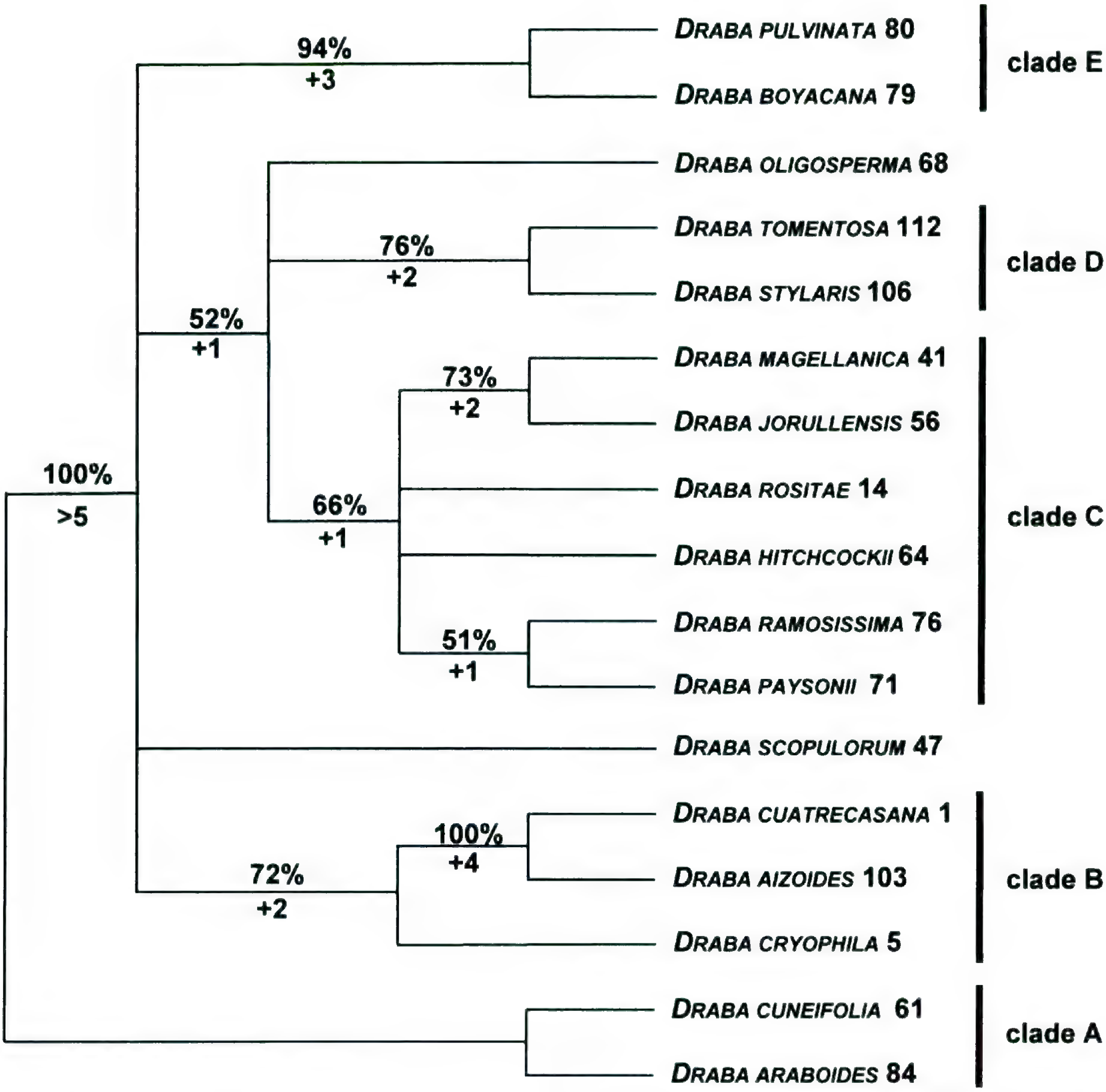

Figure 5. Strict consensus tree from Fitch parsimony using a subset of *trn*L sequences. Bootstrap support from 1000 replicates is seen above branches; decay values are indicated below branches. Accession numbers following taxa correspond to Table 1. Clades A–E correspond to *trn*L clades A–E from Figure 4.

within clade B (Fig. 4). These two plastomes of *D. aizoides* are separated by seven mutations. Some plastome types (*D. scopulorum*, acc. no. 47, *D. oligosperma*, acc. no. 68, and *D. aizoides*, acc. no. 107 from Widmer & Baltisberger, 1999b) are not supported significantly within any of the five clades A to E (Figs. 4 and 5). The plastome type of *Draba oligosperma* is positioned basal to clades C and D in distance and parsimony analyses (Figs. 4 and 5). The plastome type of *D. scopulorum* is supported within clade D by distance analysis (Fig. 4); however, this is not supported by a bootstrap value greater than 50%, and parsimony analysis with a reduced data set (Fig. 5) provided no information at all. cpDNA sequence data from *Erophila* were not available, and research of the authors focusing on annual Eurasian *Draba* is in progress.

ITS VERSUS *trn*L DATA

There is some congruence between phylogenetic trees from both data sets (Figs. 2 and 4): (1) American *D. cuneifolia* (acc. no. 61), *D. platycarpa* (acc. no. 69), *D. reptans* (acc. no. 72), and *D. araboides* (acc. no. 84) are separated from all remaining *Draba* taxa, American as well as European material, and are grouped in ITS clade I or corresponding *trn*L clade A; (2) the majority of American *Draba* is combined to ITS clade VI, which largely corresponds to *trn*L clade E; (3) taxa that were integrated

Table 3. Distribution of plastome types A–E among *Draba* accessions analyzed herein according to their sampling area. Unique or "ambiguous" plastome type of *D. scopulorum*, *D. oligosperma*, and *D. aizoides* (acc. nos. 47, 68, and 108, respectively) have been excluded here. Numbers of accessions showing a particular plastome type are indicated.

Origin of analyzed accessions	Plastome type (according to Fig. 2)				
	A	B	C	D	E
Europe		3		6	
U.S.A.	3		8		5
Peru	1				8
Venezuela		1			6
Colombia		3	1		5
Argentina			2		1
Chile			1		1
Mexico			2		3
Bolivia					2
Ecuador					10

into ITS clades IV and V possess a plastome type typical for taxa from clade C; and (4) European *Draba* is divided into two groups among both data sets (clade B and D in the plastid data set; and significant subgrouping within clade III in the ITS data set including *Erophila*), but the separation of taxa forming clades B and D does not correspond to that in the ITS clade III.

However, eight accessions (*D. pennell-hazenii*, acc. no. 3; *D. rositae*, acc. no. 14; *D. farsetioides*, acc. no. 31; *D. funiculosa*, acc. no. 33; *D. scopulorum*, acc. no. 47; *D. helleriana*, acc. no. 54; *D. oligosperma*, acc. no. 68; and *D. streptocarpa*, acc. no. 73) from America assign to different clades when both phylogenies (Figs. 2 and 4) were compared with each other. In addition, plastome types from *Draba aizoides* are found at three different positions (Fig. 4). Most American *Draba* species with ITS type VI (Fig. 2) possess a plastome type grouping into clade E (Fig. 4). However, American *Draba rositae* (acc. no. 14), *D. helleriana* (acc. no. 54), and *D. streptocarpa* (acc. no. 73) from ITS clade VI do have the plastome type C and not type E, as in the majority of taxa investigated, and within *D. pennell-hazenii* (acc. no. 3) and *D. farsetioides* (acc. no. 31) from ITS clade VI we found a plastome type from clade B. *Draba oligosperma* (acc. no. 68) from ITS clade IV (Fig. 2) and *D. scopulorum* (acc. no. 47), which is also grouped to ITS clade IV in parsimony analysis (Fig. 3), do not have the plastome type C (Fig. 4) as do the remaining taxa of ITS clade IV. However, both plastomes of these taxa, *D. scopulorum* and *D. oligosperma*, are found peripheral to plastome clade C (Fig. 4). Interestingly, American *D. funiculosa* (acc. no. 33), with an ITS type closer to European *Draba*, showed a plastome type grouping to clade E (Fig. 4).

Discussion

Status of tribe Alysseae and the phylogenetic position of genus *Draba*

Preliminary molecular phylogenetic analysis (Koch, unpublished) suggests that the morphologically poorly defined tribe Alysseae is not monophyletic. Two of Schulz's (1936) tribes, Lunarieae and Drabeae, were recognized by Janchen (1942) and Hayek (1911) as subtribes of the Alysseae. The genus *Camelina*, which was treated by Al-Shehbaz (1987) in the Alysseae, was shown by Zunk et al. (1999) to be very close to genus *Capsella*, a genus traditionally placed in the tribe Lepidieae. A majority of the 650 species of the Alysseae (sensu Janchen, Hayek, and Al-Shehbaz) belong to the genera *Alyssum* (170 spp.) and *Draba* (350 spp.). The present analysis supports a closer relationship among *Draba*, Eurasian *Arabis*, and the European *Aubrieta*. Eurasian *Arabis* and *Aubrieta* have been shown to represent a core group of the tribe Arabideae (Koch et al., 1999a). However, as traditionally delimited by Janchen (1942), Hayek (1911), or Schulz (1936), the tribe Arabideae breaks down as an unnatural group (Koch et al., 1999a) (Fig. 1). Similarily, the tribe Lepideae is not monophyletic, and several of its constituent genera are sister taxa in other tribes of the Brassicaceae (Koch et al., 2000, 2001). The consistent conclusion reached from all molecular studies of the Brassicaceae is that the tribal relationships of Schulz (1936), Janchen (1942), and Hayek (1911), which are based solely on morphological characters, are highly artificial and do not reflect phylogenetic relationships. Such artificiality was also elucidated at the generic level, especially by molecular studies on *Cochlearia* (Koch et al., 1999b), *Thlaspi* (Mummenhoff et al., 1997a, b), and *Arabis* (Koch et al., 1999a, 2000, 2001). Our findings should encourage other investigators of cruciferous genera to test phylogenetic assumptions at a higher taxonomic level.

Hybrid ITS types and reticulation

We found no ambiguous nucleotide positions when sequencing *Draba* ITS regions, although hybrid origin for several taxa is likely because of some characteristics frequently found in species groups showing hybridization and introgression: (1) incongruencies between nuclear- and plastid-de-

Table 4. References for chromosome numbers among *Draba* taxa under study. For taxa that were recognized by Schulz (1927) information about his sectional treatment is given (see also Table 2).

Sectional classification according to Schulz (1927)	Taxon	Chromosome no. and reference	Ploidy level
Not mentioned by Schulz	*D. cryophila*	$2n$ = 48 (Galland & Pfitsch, 1986b)	hexaploid
Adenodraba	*D. jorullensis*	n = 12 (Beaman et al., 1962)	triploid
Aizopsis	*D. aizoides*	$2n$ = 16 (Hess et al., 1977)	diploid
Calodraba	*D. gilliesii*	n = 24 (Boecher, 1966)	hexaploid
Chamaegongyle	*D. bellardii*	$2n$ = 48 (Galland & Pfitsch, 1986a)	hexaploid
	D. chionophila	$2n$ = 48 (Galland & Pfitsch, 1986a)	hexaploid
Chrysodraba	*D. oligosperma*	$2n$ = 32, 64 (Mulligan, 1972)	tetraploid, octoploid
	D. paysonii	$2n$ = 42 (Mulligan, 1971)	pentaploid + 2
Doliostylis	*D. pulvinata*	$2n$ = 48 (Galland & Pfitsch, 1986a)	hexaploid
Drabella	*D. crassifolia*	$2n$ = 40 (Price, 1979)	pentaploid
Leucodraba	*D. carinthiaca*	$2n$ = 16 (Hess et al., 1977)	diploid
	D. dubia	$2n$ = 16 (Hess et al., 1977)	diploid
	D. fladniziensis.	$2n$ = 16 (Hess et al., 1977)	diploid
	D. glabella	n = 32, 40 (Mulligan, 1970)	octoploid, decaploid
	D. incerta	n = 56 (Mulligan, 1966)	14-ploid
	D. ladina	$2n$ = 32 (Hess et al., 1977)	tetraploid
	D. magellanica	n = 32 (Heilborn, 1941)	octoploid
	D. stylaris	$2n$ = 32 (Hess et al., 1977)	tetraploid
	D. tomentosa	$2n$ = 16 (Hess et al., 1977)	diploid
Phyllodraba	*D. helleriana*	n = 8 (Ward, 1983), n = 9 (Ward & Spellenberg, 1988)	diploid
	D. mogollonica	n = 16 (Ward, 1983)	tetraploid
	D. ramosissima	n = 8 (Nye, 1969)	diploid
	D. streptocarpa	n = 20 (Price, 1979)	pentaploid
Rhabdodraba	*D. pickerengii*	$2n$ = 24 (Favarger & Huynh, 1965)	triploid
Tomostima	*D. cuneifolia*	$2n$ = 16 (Rollins & Ruedenberg, 1971)	diploid
	D. platycarpa	$2n$ = 32 (Rollins & Ruedenberg, 1971)	tetraploid
	D. reptans	$2n$ = 16 (Löve & Löve, 1982) $2n$ = 32 (Smith, 1965)	diploid, tetraploid

rived phylogenetic hypotheses, (2) the occurrence of polyploids (Table 2). Additionally, for European *Draba* extensive hybridization and reticulation have been shown previously (Widmer & Baltisberger, 1999a, b). Therefore, we have to assume that concerted evolution of putative ancestral ITS types resulted in one dominant ITS copy. Different modes of concerted evolution of ITS regions have been discussed, e.g., for *Gossypium* (Wendel et al., 1995a, b), roses (Vissemann, 2000), *Quercus* (Muir et al., 2001), and other plants (Buckler et al., 1997), and for some cruciferous taxa (*Hilliella*, *Cochleariella* in Koch & Al-Shehbaz, 2000; *Aradidopsis* in O'Kane et al., 1996; *Cardamine* in Franzke et al., 1998; *Microthlaspi* in Mummenhoff et al., 1997b). Sequence divergence values of ITS types from putative parents, which produced hybrids in which concerted evolution has been documented, range from 3.1 to 7.8% (Koch & Al-Shehbaz, 2000: 270). Sequence divergence values for *Draba* ITS types exceeded 9%, and these might indicate a relatively old age for the genus. Divergence time estimates of cruciferous plants are found in Koch et al. (2000) for chalcone synthase and alcoholdehydrogenase and in Koch et al. (2001) for chalcone synthase and maturase K. A comparison of these time estimates with an ITS-derived phylogeny comprising a similar set of species (Koch et al., 1999a) shows that 1% ITS sequence divergence correspond to approximately 0.5 to 1.0 million years.

American *Draba* occur at different phylogenetic positions, sometimes together with European *Draba* plastome types (Fig. 4). They include numerous polyploids (Table 4), and it is likely that hybridization and polyploidization played a major role in their evolution. In order to test this assumption and show interrelationships between different ITS types, several comparisons of three ITS sequences from three different ITS clades (Fig. 2) were done to analyze the distribution of variable nucleotides. These

American taxa compared as such are represented by asterisks in Figure 2. First, American *Draba cryophila* (acc. no. 5, clade II) was compared with *D. hitchcockii* (acc. no. 64) and *D. tucumanensis* (acc. no. 51) of clades V and VI, respectively. The distribution of nucleotide diversity revealed that *D. hitchcockii* had 21 characters in common with *D. tucumanensis* and only 5 characters with *D. cryophila* (acc. no. 5). Of the eight nucleotide positions where *D. hitchcockii* differed from *D. cryophila* and *D. tucumanensis*, three were identical to positions from *D. jaegeri* (acc. no. 66, also from clade V). Synapomorphic characters were found within the ITS2 regions of *D. tucumanensis* (acc. no. 51) and *D. hitchcockii* (acc. no. 64), but not within *D. cryophila* (acc. no. 5) and *D. hitchcockii* (acc. no. 64) or *D. jaegeri* (acc. no. 66).

Different results were obtained upon comparison of *D. jorullensis* (acc. no. 57) of clade VI (Fig. 2) with *D. tucumanensis* (acc. no. 51) and *D. hitchcockii*/*D. jaegeri* (accession nos. 64 and 66). In this case, both *D. hitchcockii* and *D. jaegeri* shared five characters with *D. jorullensis* (acc. no. 57) and seven with *D. tucumanensis* (acc. no. 51). Three of eight characters of *D. hitchcockii* (acc. no. 64), which were not found in *D. tucumanensis* (acc. no. 51) and *D. jorullensis* (acc. no. 57), were synapomorphic with those of *D. jaegeri* (acc. no. 66). Furthermore, *D. tucumanensis* (acc. no. 51) contributed to all variable nucleotide positions in the ITS2 region shared with either *D. hitchcockii* (acc. no. 64) or *D. jaegeri* (acc. no. 66), whereas *D. jorullensis* (acc. no. 57) contributed nucleotide positions only within the ITS1 region. These findings are interpreted as the result of hybridization between taxa of clades IV and VI, as represented by *D. tucumanensis* and *D. jorullensis*, respectively, which produced the hybrid ITS types found in clade V as represented by *D. hitchcockii* and *D. jaegeri* (Fig. 2).

Four additional comparisons are made to test the possible role of hybridization in the formation of ITS types of clade VI (Fig. 2) that includes no European taxa: (a) *D. cryophila* (acc. no. 5, clade II), *D. jorullensis* (acc. no. 57, clade VI), and *D. tucumanensis* (acc. no. 51, clade IV); (b) *D. cryophila* and *D. helleriana* (acc. nos. 5 and 54, basal in clade VI), and *D. tucumanensis* (acc. no. 51, clade IV); (c) *D. tucumanensis* and *D. jorullensis* (acc. nos. 51 and 57) and *D. helleriana* (acc. no. 54); as well as (d) *D. cryophila*, *D. helleriana*, and *D. jorullensis* (acc. nos. 5, 54, and 57, respectively).

The first two comparisons (first, among acc. nos. 5, 51, 57, and second, among 5, 51, 54) revealed that accessions 54 and 57 had only 6 characters in common with accession number 5 of clade II but 23 characters with accession number 51 of clade IV. The third comparison (acc. nos. 51, 54, and 57) revealed that all synapomorphic characters combined exclusively accession numbers 54 and 57. This might indicate close relationships of taxa from clade VI, which includes accession numbers 54 and 57, and a monophyletic origin. The fourth comparison (acc. nos. 5, 54, and 57) provides no additional data toward the hybridization of taxa from either clade II or IV as a source for ITS types found in clade VI. Accession number 54 shared only 3 characters with accession number 5, but accession number 54 shared 21 characters with accession number 57. Therefore, based on ITS sequences, it was not possible to verify the hypothesis that ITS types from clade VI evolved via concerted evolution after hybridization.

Comparison of the maternal plastid phylogeny (see taxa indicated by black arrows, Fig. 4) with the ITS-derived phylogeny indicates that plastome types found in *D. pennell-hazenii* (acc. no. 3) and *D. farsetioides* (acc. no. 31) similar to those found in European taxa (plastid clade B) are distributed among accessions with an ITS type of clade VI. By contrast, *D. funiculosa* (acc. no. 33) has a plastome type found in clade E, but its ITS copy is related to European ITS types found in ITS clade III. Plastome types from plastidic clade C (*D. rositae*, *D. helleriana*, and *D. streptocarpa* or acc. nos. 14, 54, 73, respectively) contributed to the genetic constitution of taxa found in ITS clade VI. Interestingly, plastome type E, which is distributed among American *Draba* of the ITS clade VI, is similar to a plastome type from the European *D. aizoides* (acc. no. 108, Fig. 4) but not from the other accessions of *D. aizoides* (acc. nos. 107, 109, 103), which assort to plastome clades B and D. Extensive intraspecific cpDNA haplotype variation in alpine *D. aizoides* was demonstrated by Widmer and Baltisberger (1999b). Therefore, one could speculate that ancient gene flow and chloroplast capture might have resulted in the similar transmission of European plastome types into American *Draba* and in the constitution of the whole complex of taxa with an ITS type from clade VI. Plastome types found in taxa from this group mostly belong to plastome type E (only 5 out of 51 accessions with ITS type VI have been shown to possess other plastome types than plastome type E) and are only weakly differentiated from each other. There is no resolution within clade E in the *trn*L-derived phylogeny.

Taking both approaches into account, the comparison of ITS types and the distribution of plastome types among different clades reveals strong

evidence for extensive reticulation during the evolution of the American complex of *Draba*. However, concerted evolution of ITS types has resulted in homogeneous ITS copies within single taxa: no difficulties were encountered while obtaining the sequences by direct cycle sequencing of the purified PCR products. The genetic source of plastome and ITS type variation probably originated from Eurasian taxa, for which very complex evolutionary scenarios have already been described. Subsequent hybridization probably took place among different groups of American *Draba* (e.g., taxa from ITS clade II with taxa from ITS clade IV resulted in taxa from ITS clade V), and some taxa from the ITS clade VI crossed back with taxa from clades V or IV possessing plastomes of type C. Only taxa from ITS clade I (corresponding to *trn*L clade A), all of which are distributed in America, represent a genetically separated lineage (Figs. 2, 4).

These hypotheses might be simplified; however, they will become more complex when additional individuals from a single taxon or one population are analyzed. For example, extensive ongoing gene flow has been reported within *Draba* from the Alps and Scandinavia (Widmer & Baltisberger, 1999a, b; Brochmann et al., 1992a–d; Brochmann et al., 1993). Although the study of herbarium material is greatly affected by undersampling, it is rather remarkable that in 8 out of the 74 samples of American *Draba* (> 10%) analyzed, incongruencies between ITS- and *trn*L-derived phylogenies were detected. One has to assume that much higher levels of incongruencies will be observed in genetic analyses at the populational level.

SECTIONAL CLASSIFICATION OF *DRABA*

Draba is generally recognized as a natural genus of about 350 species distributed primarily in the Arctic, subarctic, and alpine regions of the Northern Hemisphere, with about 65 species in South America along the Andes from Colombia to Patagonia (Al-Shehbaz, 1987). In the present study we focused on American *Draba*, including a limited number of species from Europe (8 species from 10 accessions). Eleven species grow in Mexico and Central America (Rollins, 1984). More than 100 grow in North America and Greenland (Rollins, 1993), with the ranges of about 20 of these extending into the Arctic and subarctic Eurasia.

Schulz (1927, 1936) divided *Draba* (excluding *Erophila*) into 17 sections (Table 2) that have been considered by some (e.g., Fernald, 1934; Al-Shehbaz, 1987) to be highly artificial. Schulz defined his sections primarily on the presence or absence of stem leaves, flower color (white vs. yellow), the presence or absence of median nectaries, and style length. Four of Schulz's sections are no longer recognized in *Draba*. Section *Helicodraba* O. E. Schulz was shown by Hyam and Jury (1990) to belong to the Southwest Asian *Graellsia* Boiss. Section *Nesodraba* (Greene) N. Busch was reduced by Berkutenko (1995) to *Schivereckia* Andrzeiowski ex DC. Sections *Tomostima* (Raf.) O. E. Schulz and *Abdra* (Greene) O. E. Schulz are believed to form the well-defined genus *Tomostima* Raf. (Price & Al-Shehbaz, unpublished). Species as assigned to the remaining sections are still maintained in the genus and are not currently questioned (Table 2). Section *Acrodraba* O. E. Schulz (1 species, *Draba oreadum* Maire) is restricted to northern Africa, whereas sections *Rhabdodraba* O. E. Schulz (10 species), *Adenodraba* O. E. Schulz (9 species), *Tylodraba* O. E. Schulz (8 species), *Dolichostylis* (Turcz.) O. E. Schulz (3 species), *Calodraba* O. E. Schulz (14 species), and *Chamaegongyle* O. E. Schulz (6 species) are distributed in Central and South America. With the exception of section *Aizopsis* DC. (28 species), which is almost exclusively European, larger sections include the North American and Eurasian *Chrysodraba* DC. (57 species), the North American and East Asian *Phyllodraba* O. E. Schulz (29 species), European and central Asian *Leucodraba* DC. (59 spp.), and the Asian *Drabella* DC. (23 spp.). The last included two South American species that doubtfully belong there.

Four out of the 17 sections sensu Schulz (1927), which comprise only five species (1.5% of the total in *Draba*), were not included in the present study. Sections *Helicodraba* and *Nesodraba* (4 species) have already been combined under different genera as outlined above. Material of the North American section *Abdra* (1 species) and African section *Acrodraba* (1 species) were not available. Schulz's sectional classification is given in Roman numerals in parentheses in the phylogenetic ITS tree (Fig. 2).

The phylogenetic analysis of the ITS sequence data (Fig. 2) shows that all sections exclusively distributed in South and Central America (Table 2, sects. *Rhabodraba*, *Tylodraba*, *Calodraba*, *Dolichostylis*, *Adenodraba*, *Chamaegongyle*) fall within clade VI. This clade also includes such taxa as *Draba aureola* (acc. no. 101) of section *Phyllodraba* (North America, Asia), *D. crassifolia* (acc. no. 59) from section *Drabella* (Eurasia, North America), and *D. cruciata* (acc. no. 60) of section *Chrysodraba* (Eurasia, North America). This suggests that South and Central American *Draba* probably evolved from other sections distributed in the Northern Hemisphere. With our molecular data it is difficult

to distinguish possible, relatively recent South-North migration events (from South America to the North) from the earlier North-South migration route. However, in this case some morphologically defined species should have a much wider distribution range, which is not the case.

A few species from exclusively South and Central American sections fall within other clades. For example, *Draba bellardii* (acc. no. 7) of section *Chamaegongyle* belongs to the ITS clade II, whereas both *D. scopulorum* (acc. no. 47) of section *Rhabdodraba* and *D. gilliesii* (acc. no. 34) of section *Calodraba* belong to clade IV.

Some level of congruence was found when comparing the ITS clustering of European *Draba* with the sectional classification of Schulz (1927, 1936). Taxa comprising the ITS clade III were assigned to sections *Aizopsis*, e.g., *D. aizoides*, and *Leucodraba*, e.g., *D. tomentosa*. These sections are primarily Eurasian. Interestingly, *D. funiculosa* (acc. no. 33) falls within this ITS clade, but the extremely long branch (more than twice longer than the maximum distance found within the total ingroup) that sets it off from the remaining European taxa indicates that its ITS type has considerably diverged. This particular subantarctic species comprises the monotypic section *Linodraba*.

A comparison of Schulz's (1927, 1936) sectional classification with the present molecular study reveals that section *Tomostima* (XVI, Table 2), which corresponds to the ITS clade I (Fig. 2) and *trn*L clade A (Fig. 4), is the most clearly supported.

Schulz (1927, 1936) and all European taxonomic treatments maintained *Erophila* as a distinct genus that is closely related to *Draba*. However, the present ITS data show that it is better integrated into *Draba*, and these results support the view held by most North American botanists (e.g., Fernald, 1934; Al-Shehbaz, 1987; Rollins, 1993). The only morphological difference between *Erophila* and *Draba* is the presence of bifid petals in *Erophila* rather than entire to deeply lobed ones in *Draba* (Al-Shehbaz, 1987).

In conclusion, our findings do not provide much support for Schulz's (1927, 1936) sectional classification, although they suggest some species tentatively correspond to a few of his sections. However, several taxa (*D. pennell-hazenii*, *D. rositae*, *D. farsetioides*, *D. funiculosa*, *D. scopulorum*, *D. helleriana*, *D. oligosperma*, and *D. streptocarpa*, acc. nos. 3, 14, 31, 33, 47, 54, 68, 73, respectively), which fall into different clades when the ITS- and *trn*L-derived phylogenies were compared, indicate extensive cross relationships not only among taxa of primarily South and Central American sections, but also among sections with other geographical centers of distribution, e.g., North America, Europe (Eurasia), and the subantarctic. A case in point is the South American *Draba magellanica* from Argentina (sect. *Leucodraba*, XIV), which has a chloroplast type (clade C, Fig. 4) not found within the remaining species of this section (e.g., *D. dubia* within *trn*L clade D). Two other species from Argentina (*D. funiculosa*, acc. no. 33, and *D. magellanica*, acc. no. 41) have chloroplast types E and C, respectively.

Although one might argue that in order to achieve a better understanding of the sectional classification within *Draba*, more analyses are needed, especially from the sections not included in the present study, it is safe to conclude that our molecular data clearly show that the conventional sectional classification of *Draba* as conceived by Schulz (1927, 1936) is an artificial one.

CHROMOSOME NUMBER, POLYPLOIDY, AND APOMIXIS

Because the present study is based on herbarium material, no chromosome counts were made from the plants investigated. However, several chromosome counts are available from the literature (Table 4). From this, it seems likely that the base chromosome number for *Draba* is $x = 8$. This is also the base chromosome number for sister European genera *Arabis* and *Aubrieta* (Fig. 1). Chromosome data demonstrate the existence of diploid, triploid, tetraploid, pentaploid, hexaploid, octoploid, and decaploid taxa based on $x = 8$ (Table 4). Higher chromosome numbers ($2n = 112$) have been reported for *D. incerta* (acc. no. 65) from North America (sect. *Leucodraba*).

The well-defined clade I (ITS data), or corresponding clade A (*trn*L data), comprising *D. cuneifolia* (diploid, acc. no. 61), *D. platycarpa* (tetraploid, acc. no. 69), *D. reptans* (diploid and tetraploid, acc. no. 72), and *D. araboides* (no count for chromosome number, acc. no. 84), included diploid and tetraploid species (Table 4). In summary, this clade (well defined as sect. *Tomostima*, XVI) comprises mostly diploid species (as known so far), and also represents an ancestral clade to all remaining *Draba*. This finding will need further investigation because section *Tomostima* is restricted to North and South America, and it is hard to believe that these taxa served as ancestors for Eurasian *Draba*. The consequence is the recognition of genus *Tomostima* (Price & Al-Shehbaz, unpublished).

The ITS data indicate a hybrid origin for *Draba*

ramosissima (clade V, acc. no. 76, Fig. 2), a species reported to be diploid (Table 4). As outlined before, direct ITS sequence comparisons demonstrated that ITS types from clade V most likely evolved from ancestral ITS types of clades VI and IV. Therefore, in *D. ramosissima* speciation via hybridization must have taken place at the diploid level and only diploid parental taxa could have served as progenitors. Another diploid, *D. helleriana* (acc. no. 54) has an ITS type corresponding to clade III (Figs. 2, 3, 6) and a plastome type to clade C (Figs. 4–6). This incongruency could be best explained by gene flow between different groups of taxa, thus indicating another hybrid speciation at the diploid level. Except for *D. cuneifolia* and *D. reptans* from section *Tomostima* and *D. helleriana* and *D. ramosissima* from section *Phyllodraba*, counts for the remaining American *Draba* species showed polyploidy (Table 4). By contrast, triploids (*D. jorullensis*, acc. no. 56; *D. pickerengii*, acc. no. 44), pentaploids (*D. crassifolia*, acc. no. 59; *D. streptocarpa*, acc. no. 73), and an aneuploid (*D. paysonii*, pentaploid + 2 chromosomes, acc. no. 71) have been reported (Table 4), and these taxa grouped to plastidic clades C and D or ITS clades IV and VI.

Apomixis has been documented in a few species such as *Draba verna* or *D. oligosperma* (Mulligan & Findlay, 1970; Mulligan, 1971, 1972, 1976; Price, 1980), and it is likely that it might be more widespread among American *Draba*. Therefore, in *Draba* apomixis might be an additional mechanism that led to the recognition of several hundred, morphologically defined taxa. The occurrence of apomixis has also been documented for other Brassicaceae, and North American *Arabis* parallels the situation in *Draba* (Böcher, 1966; Rollins, 1983). North American *Arabis*, from which many species were more appropriately transferred to *Boechera* (Löve & Löve, 1975; Weber, 1982, 1989), is a young taxon, presumably of Pleistocene origin. This genus exhibits remarkable morphological, ecological, and physiological diversification leading to the recognition of more than 50 species, and most of them show the trait apomixis.

As suggested by the low sequence divergence values, American *Draba* either of the ITS clade VI (Fig. 2) or the corresponding *trn*L clade E (Fig. 4) probably are relatively young taxa similar to *Boechera*. Comparable low levels of molecular variation have been found separating the North and South American *Noccaea* Moench, sensu Meyer (1973, 1979), or American *Thlaspi* L. sensu lato from their Eurasian relatives (Koch et al., 1993; Koch et al., 1998c). Contrary to this, in Europe several plastome types from *D. aizoides* were found by Widmer and Baltisberger (1999b), some of them very close to *D. aizoides*, accession number 107 (DA2, DA3, DA9, DA6, DA8, Widmer & Baltisberger, 1999b), separated by a maximum of seven mutations (in this analysis corresponding to clade B, Fig. 5), and one plastome type (DA7) was separated from *Draba aizoides*, acc. no. 108, by two mutations. All samples analyzed by Widmer and Baltisberger (1999b) originated from the Swiss Alps and demonstrate the enormous plastome variation even within one taxon (*Draba aizoides*) from a restricted area. ITS sequence variation among *D. aizoides* accessions (Fig. 2) is much lower, and all *D. aizoides* accessions analyzed herein confined to one group within ITS clade III. In this group we also found one *D. ladina* (acc. no. 116); this is not unexpected, because this taxon evolved by hybrid speciation involving *D. aizoides* as one parental taxon (Widmer & Baltisberger, 1999a).

The close relationships between the floras of Central Asia and western North America are well documented (Parks & Wendel, 1993, and references therein). The putative Bering bridge connected Asia and North America several times throughout the late Tertiary and Pleistocene (Parrish, 1987), and this land bridge probably served as an immigration route for several Brassicaceae, including *Thlaspi* (Payson, 1926) and *Stroganowia* Karelin & Kirilov (Rollins, 1982). Palynological analyses from the Venezuelan Andes document the occurrence of *Draba* in Holocene deposits after late Pleistocene deglaciation events (Salgado Labouriau et al., 1988).

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EVIDENCE FOR MOTH AND BUTTERFLY POLLINATION IN *GLADIOLUS* (IRIDACEAE–CROCOIDEAE)[1]

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Abstract

Pollination strategies of *Gladiolus*, one of the largest genera of the monocot family Iridaceae, are unusually diverse, and include various bee species, foraging either for nectar or for pollen, passerine birds, long-proboscid flies foraging for nectar, hopliine beetles that use the flowers primarily as sites for assembly, and Lepidoptera. Pollination by insects of this order comprises two entirely different sets of pollinators, night-flying moths (Noctuidae or Sphingidae) and butterflies (evidently only one species of Satyridae). These lepidopteran-pollinated flowers have quite different floral adaptations and both types are specialist systems, although moth flowers may be pollinated by a range of different moths. In *Gladiolus* moth-pollinated flowers are usually large, long-tubed and pale-colored, or mottled dull purple to brown, are usually richly scented, often open fully only at night, and produce relatively concentrated nectar that is sucrose-rich. Butterfly flowers, in contrast, are fully open during the day, close partially or completely at night, are often bright crimson to scarlet, usually with prominent white splashes on the lower tepals, but are also large, have a long tube, and produce quantities of relatively dilute nectar, either sucrose-rich or hexose-rich. Comparing the pollination systems of related species, we infer that night-flying moth pollination arose 6 times in the genus, whereas butterfly pollination arose 3 times in the 165 species of southern Africa, and that the two lepidopteran pollination systems in *Gladiolus* arose quite independently of one another.

Key words: butterflies, floral ecology, *Gladiolus*, Iridaceae, moths, nectar, pollination systems.

Pollination in the approximately 35 genera of the Iridaceae of sub-Saharan Africa, where over 1000 species of the family occur, is remarkably diverse. Across the continent pollination systems include four orders of insects (Coleoptera, Diptera, Hymenoptera, Lepidoptera) and passerine birds, as well as facultative, and possibly obligate autogamy. Pollination by insects of the orders Diptera, Hymenoptera, and Lepidoptera is itself diverse, involving a range of families of each order and different sets of floral adaptations and associated rewards to pollinators. Here we present evidence for two different pollination strategies utilizing Lepidoptera in the large, predominantly African genus *Gladiolus*. Elsewhere we have documented passive pollination in the genus by large-bodied apid-anthophorine bees (Goldblatt et al., 1998a), hopliine beetles (Goldblatt et al., 1998b), long-proboscid flies in the families Nemestrinidae and Tabanidae with elongate mouth parts exceeding 15 mm (Goldblatt & Manning, 1999, 2000), and an active pollination system involving pollen-collecting female bees (Goldblatt et al., 1998a). We have also presented evidence for passerine bird pollination in *Gladiolus* and reviewed pollination systems for the entire genus (Goldblatt et al., 1999, 2001). By comparing and contrasting the evidence for moth versus butterfly pollination in *Gladiolus*, we show just how different the two systems are that use lepidopteran pollen vectors.

Pollination by large butterflies, so far in *Gladiolus* known to involve only the satyrid, *Aeropetes tulbaghia*, has already been demonstrated for two species of *Gladiolus* and was inferred for several more because of the distinctive floral features present in species pollinated by this butterfly (Johnson & Bond, 1994). These features include a large, unscented flower, bright red perianth often with white splashes on the lower tepals, a narrow but fairly long perianth tube, and the presence of large quantities of nectar (Johnson & Bond, 1994; Goldblatt & Manning, 1998). Night-flying moth pollination has been inferred for nine species of *Gladiolus* based on the presence of features commonly asso-

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ciated with moth pollination, including a pale-colored perianth, presence of fairly concentrated nectar, and a strong, often distinctive scent with a clove component, and in some species floral odor produced only at night (Goldblatt & Manning, 1998). Field observations and investigation of floral features allow us to expand our understanding of these pollination systems. Moreover, by using information about phylogenetic relationships in the genus and comparing the pollination systems of related species, we can infer the number of times that each system evolved within the genus and suggest ancestral species, thus developing hypotheses about the evolution of the floral traits associated with pollination by different Lepidoptera.

Materials and Methods

species examined

Observations on the floral and pollination biology of *Gladiolus* were made during the years 1993 to 1999 in the field in southern Africa and in living collections at the Missouri Botanical Garden, St. Louis, and Kirstenbosch Botanic Gardens, Cape Town. Together with our research on the systematics of the genus (Goldblatt & Manning, 1998; Manning et al., 1999), we have identified 20 species that have flowers likely to be pollinated by Lepidoptera from a total of 165 species of *Gladiolus* that occur south of the Limpopo–Cunene River axis. At least an additional 15 species of tropical Africa (Goldblatt, 1996) have similar flowers and may be assumed to be pollinated by Lepidoptera. Southern African species fall in five of the seven sections recognized in the genus by Goldblatt and Manning (1998: sects. *Blandus, Hebea, Homoglossum, Linearifolius,* and *Ophiolyza*). Species in two additional sections of the genus, sections *Acidanthera* and *Decoratus,* in tropical Africa also exhibit features consistent with pollination by Lepidoptera.

Candidates for Lepidopteran pollination were recognized by two separate suites of characters. The first is the classic syndrome for moth pollination (Faegri & van der Pijl, 1979) in which pale flower color and production of a strong, rich odor are associated with some features only exhibited at night. In *Gladiolus* such flowers are usually large, have an elongate floral tube, shortly exserted unilateral stamens, and the strong floral odor is often produced or intensified at night. Pigmentation may be cream or whitish, but several species have darkly mottled to nearly uniformly dark brown perianths. A second syndrome of characters, described in detail by Johnson and Bond (1994), combines bright red floral pigmentation, a large flag-like presentation, absence of floral odor, and often lower tepals marked with white splashes (we use the term tepal for perianth lobe here).

seasonality, floral phenology, longevity, and floral presentation

Direct phenological observations are presented on 18 southern African species of *Gladiolus* made during the years 1993 to 1998 in the field (Table 1) and in living collections at Kirstenbosch Botanic Gardens, Cape Town. Observations include mode and timing of anthesis (i.e., opening of individual buds), anther dehiscence, expansion of stigmatic lobes, followed by withering of the perianth. Data on seasonality are taken from Goldblatt and Manning (1998). Compatibility relationships were not examined for the study. Plant vouchers (Table 1) are deposited at the Missouri Botanical Garden Herbarium, St. Louis (MO), and/or the Compton Herbarium, Cape Town (NBG).

nectar analysis

Nectar volume measurements were taken from unbagged flowers in the field, reflecting both rates of secretion and depletion, and from plants maintained in the laboratory, and not visited by insects (effectively representing bagged flowers). Experience with Iridaceae has shown that nectar characteristics gradually change in species retained in water for periods greater than 24 hours, the nectar usually becoming more diluted (Goldblatt et al., 1995). Nectar from flowers on cut stems maintained in water in the laboratory was therefore sampled within 18 hours. To collect nectar whole flowers were picked and nectar was withdrawn from the base of the perianth tube with 3 μl capillary tubes after separating the ovary from the perianth base (perianth tubes are too elongate and curved to allow nectar removal directly via the mouth of the tube with a capillary tube). Detaching the perianth from the top of the ovary causes minimal damage, and contamination of nectar by fluid from broken tissue is not significant given the large volumes of nectar produced by flowers of species under investigation. The percentage of sucrose equivalents in fresh nectar was measured in the field or laboratory on a Bellingham and Stanley hand-held refractometer (0–50%) from five or more individuals per population, unless fewer individuals were available. Additional nectar samples were dried on Whatman filter paper no. 1 and analyzed by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, using HPLC sugar analysis.

Table 1. Study sites and voucher information for species studied. Vouchers are housed at MO (Goldbatt) or at NBG (other collectors). All study sites are in South Africa.

Species	Study site and voucher
GLADIOLUS* SECTION *BLANDUS	
series *Blandus*	
G. cardinalis Curt.	W Cape, near Bain's Kloof, Jan., *Goldblatt & Manning s.n.* no voucher
G. carmineus C. H. Wright	W Cape, cliffs at Hermanus, Feb., *Goldblatt 11292*
G. insolens Goldblatt & J. C. Manning	W Cape, Piketberg, Jan., *Goldblatt & Manning 10166*
G. stefaniae Oberm.	W Cape, Potberg, Mar., *Goldblatt & Manning 10176*
G. sempervirens G. J. Lewis	E Cape, Tsitsikamma Mts., May, *Manning s.n.* no voucher
GLADIOLUS* SECTION *LINEARIFOLIUS	
series *Linearifolius*	
G. emiliae L. Bolus	W Cape, near Swellendam, Mar., *Manning 1057*
	W Cape, near Riviersonerend, Mar., *Stayner s.n.*
G. guthriei F. Bolus	W Cape, Bain's Kloof, May, *Manning 1080*
G. nerineoides G. J. Lewis	W Cape, Helderberg Reserve, Somerset West, Jan., *Runnals 463*
	W Cape, Jonkershoek Mts., Jan., *Esterhuysen 32847*
***GLADIOLUS* SECTION HEBEA**	
series *Permeabilis*	
G. robertsoniae F. Bolus	Mpumalanga, near Morgenzon, Oct., *Goldblatt & Manning 10071*
***GLADIOLUS* SECTION HOMOGLOSSUM**	
series *Gracilis*	
G. albens Goldblatt & J. C. Manning	E Cape, near Grahamstown, Mar., *Dold & Weeks s.n.*
G. maculatus Sweet	W Cape, Simonstown, June, *Manning s.n.* no voucher
	Devil's Peak, May, *Manning s.n.* no voucher
G. recurvus L.	W Cape, Helderberg Reserve, Nov., *Runnals 513*
series *Tristis*	
G. hyalinus Jacq.	W Cape, Gydo Pass, Sep., *Goldblatt & Manning 9743A*
	W Cape, Lion's Head, Aug., *Barker 3861*
G. liliaceus Houtt.	W Cape, Fairfield, Caledon, Sep., *Nänni s.n.* no voucher
G. longicollis Baker	Mpumalanga, Long Tom Pass, Feb., *Goldblatt & Manning 9822*
G. tristis L.	W Cape, near Bredasdorp, Aug., *Barker 2844*
GLADIOLUS* SECTION *OPHIOLYZA	
series *Oppositiflorus*	
G. cruentus T. Moore	KwaZulu-Natal, Hillcrest, Jan., *Goldblatt & Manning 9854*
G. saundersii J. D. Hook.	E Cape, Naude's Nek, Feb., *Goldblatt & Manning 9550*

Additional species with similar flowers, assumed to be adapted for pollination by *Aeropetes* or night-flying moths, include *G. acuminatus* F. Bolus (putatively moths) and *G. stokoei* G. J. Lewis (putatively butterflies), but we have no field observations of the floral ecology of these species. We also lack observations of insect visitors for *G. albens*, *G. carmineus*, *G. cruentus*, *G. hyalinus*, *G. insolens*, and *G. robertsoniae*, but those species are included above because we have nectar and other data from study populations.

FRAGRANCE

Floral scent was noted with the human nose in the field and in cultivated plants. Presence of scents too weak to be discerned in the open air was recorded after individual flowers were picked and placed in clean, lidded glass jars and stored in a warm place. The contents of each jar was sniffed after a minimum of 60 minutes (Buchmann, 1983). The site of scent production was examined by immersing flowers in aqueous neutral red stain. Scent chemistry was examined by R. Kaiser, Givaudan-Roure Research Ltd., Switzerland, by gas chromatography using a DB-Wax Capillary column (Kaiser, 1993). Scents were captured in capsules through which air was drawn by a vacuum pump from a small, lidded chamber containing open flowers.

POLLINATION MECHANISMS AND POLLEN LOAD ANALYSES

Observations of insects on *Gladiolus* flowers involved at least 5 hours total per species and in some cases up to 20 hours total per species. For species inferred to be pollinated by moths, an additional 4 hours of observation was made per species during daylight hours to determine whether diurnal visits by insects might also occur. Observations included mode of foraging and whether insects contacted anthers and stigmas during vis-

its to flowers. Study populations always included at least 20 individuals at evidently undisturbed field sites. Insects observed to probe the floral tube or to brush the anthers or stigmas were netted when possible and, in the case of moths, then immobilized in a jar using ethyl acetate fumes. To prevent contamination of the body of an insect with pollen carried by another in the same jar, the bodies of insect specimens were isolated from each other by wrapping them in tissue prior to pinning. Individual butterflies were netted for measuring and observation of sites of pollen deposition and then released. Body length and proboscis length of insects was recorded from captured specimens. Body length was measured from the base of the labrum to the tip of the abdomen. Mouth-part length was measured from the base of the labrum to the tip of the proboscis. Night-flying moths are not easily captured simply because darkness makes them difficult to locate. Use of flashlights covered with translucent red cellophane paper for illumination significantly assisted observation and netting of moths. Captured moths were identified by Douglas Kroon (Sasolburg, South Africa), and both moth and butterfly voucher specimens were deposited with the South African Museum, Cape Town.

Identification of pollen on insect bodies was done by gently removing grains from the body surface with a dissecting needle. The residue from needle probes was collected on glass slides and mounted in 1–2 drops of Calberla's fluid (Ogden et al., 1974). Pollen grains were identified microscopically by comparison with reference to pollen grain preparations made from plants flowering at study sites. *Gladiolus* pollen grains are recognized by their large size, monosulcate aperture with prominent 2-banded operculum, and perforate-scabrate exine (Goldblatt et al., 1991).

Results

Seasonality, floral phenology and longevity, and floral presentation (Table 2)

Flowering times in the *Gladiolus* species of southern Africa that are pollinated by night-flying moths show no obvious association with their geographic ranges in the summer- or winter-rainfall zones of southern Africa (Goldblatt & Manning, 1998). Flowering of the flora peaks in late spring (September to November) in the winter-rainfall zone but in summer and early autumn (December to March) in the summer-rainfall zone. This coincides with the middle or end of the period of optimal plant growth, during or soon after the main rainy periods. In the summer-rainfall zone, *G. longicollis* flowers early in the season, mostly October and November, sometimes producing a second flowering flush in December–January. The only other species of the region showing adaptation for moth pollination blooms in spring before the first rainfall of the wet season. This is out of phase with the main flowering period for *Gladiolus* in the summer-rainfall zone (Goldblatt & Manning, 1998).

In the winter-rainfall zone, *Gladiolus hyalinus*, *G. liliaceus*, and *G. tristis* follow the main flowering pattern for the region, but *G. albens* and *G. maculatus* flower early in the season, in autumn or winter, and *G. recurvus* flowers in late winter or early spring. Flowering out of phase with the flowering peak is also characteristic of the two moth pollinated species of section *Linearifolius*, *G. emiliae* and *G. guthriei*, which flower mainly in April and May, although vegetative growth in these two species is delayed until the winter and spring when leaves are produced.

Flowering of butterfly-pollinated species of *Gladiolus* is always from late December to April, exceptionally May, and this is when the only butterfly so far recorded on *Gladiolus* species, *Aeropetes*, is on the wing (Johnson & Bond, 1994). This means that for the butterfly-pollinated species of the winter-rainfall zone, flowering occurs several months out of phase with the main growth and flowering peak for the region. As a consequence these species must also have special ecological adaptations to support the unusual flowering patterns. These may be a specialized habitat, such as cliffs, stream banks, or waterfalls (*G. cardinalis*, *G. insolens*, *G. sempervirens*), or a growth pattern in which leaf production occurs when conditions are suitable, later in the season (*G. carmineus*, *G. stefaniae*), or both (*G. nerineoides*, *G. stokoei*).

Population density appears to be moderately diffuse, and plants form extended populations with flowering individuals standing 1–3 m apart. Species of specialized habitats such as *Gladiolus tristis* (moist to marshy sites), *G. cardinalis* (waterfalls), *G. carmineus* (coastal sandstone cliffs), *G. sempervirens* (seeps and wet forest margins) may be locally common and grow in dense stands.

The pattern of flower buds opening on an inflorescence is acropetal. In all species, a mature bud expands in the early to mid morning, and the open flower typically lasts four days in *Gladiolus* species (Goldblatt et al., 1998a; Goldblatt & Manning, 1999). In moth-pollinated *Gladiolus* species flowering lasts longer. Flowers of a cultivated sample of *G. tristis* lasted five or six days, and flowers of *G. recurvus* lasted five to nine days. Flowers usually open one to two days apart, and hence there are

Table 2. Floral and phenological data for southern African *Gladiolus* species with flowers adapted for pollination by Lepidoptera. Species are arranged taxonomically according to Goldblatt and Manning (1998). Perianth tube length was recorded at study sites and may not represent the range for the species. An asterisk (*) indicates species flowering out of phase with the peak flowering time for the rainfall zone.

Species	Flower color	Perianth tube (mm)	Scent	Main flowering time	Rainfall zone
GLADIOLUS* SECTION *BLANDUS					
series *Blandus*					
G. cardinalis	red, white streaks on lower tepals	32–40	none	late Dec.–Feb.	winter*
G. carmineus	crimson-pink, white streaks on lower tepals	30–35	none	Feb.–Mar.	winter*
G. insolens	scarlet-red	ca. 38	none	Jan.–Feb.	winter*
G. stefaniae	red, white streaks on lower tepals	35–45	none	Mar.–Apr.	winter*
G. sempervirens	red, white splashes on lower tepals	25–42	none	Mar.–May	winter*
GLADIOLUS* SECTION *LINEARIFOLIUS					
series *Linearifolius*					
G. emiliae	densely brown speckled	32–45	strong fruity	Mar.–Apr.	winter*
G. guthriei	dull purple-brown	20–27	sweet-clove	Mar.–June	winter*
G. nerineoides	scarlet	25–31	none	Jan.–Mar.	winter*
G. stokoei	carmine-red	30–35	none	Mar.	winter*
GLADIOLUS* SECTION *HEBEA					
series *Permeabilis*					
G. acuminatus	cream	16–22	sweet-floral	Aug.–Sep.	winter
G. robertsoniae	white	28–44	sweet-clove	Sep.–Oct.	summer*
GLADIOLUS* SECTION *HOMOGLOSSUM					
series *Gracilis*					
G. albens	white-cream	45–60	acrid-metallic	Mar.–May	winter*
G. maculatus	cream, heavily speckled brown to dull purple	23–35	sweet-floral	May–July	winter*
G. recurvus	cream to pale pink	27–36	sweet-clove	July–Sep.	winter
series *Tristis*					
G. hyalinus	cream speckled brown, purple or green	25–26	usually odorless or sweet-clove	Sep.–Nov.	winter
G. liliaceus	beige, buff or pale orange, light mauve at night	40–45	strong sweet-clove at night	Aug.–Nov.	winter
G. longicollis subsp. *longicollis*	cream, lightly speckled	100–110	strong sweet-clove at night	Sep.–Nov.	summer*
platypetalus	white to cream	85–110	strong sweet-clove at night	Oct.–Dec.	summer*
G. tristis	white to cream	40–60	strong sweet clove at night	Sep.–Nov.	winter
GLADIOLUS* SECTION *OPHIOLYZA					
G. cruentus	red, white on lower tepals	ca. 28	none	Jan.–Feb.	summer
G. saundersii	red, white on lower tepals	33–37	none	Feb.–Mar.	summer

often two or more flowers open at any time on an inflorescence of three or more flowers. Flowers of moth-pollinated species are usually partly closed or at least the tepals are flaccid during the day, and open fully at sunset when the tepals become firm and fully extended. In species of *Gladiolus* series *Tristis* of section *Homoglossum* scent is released at the same time, although a faint odor may be detected during the day.

The reverse pattern holds for butterfly-pollinated species. At sunset, the tepals of most species partly or fully close, the tepals then loosely enclosing the exserted anthers and stigmas. During the day the tepals become fully expanded again.

Flowers of many *Gladiolus* species have been found to exhibit mechanical protandry (Scott Elliot, 1891; Goldblatt et al., 1998a; Goldblatt & Manning, 1999), and the species studied here conform

to this pattern. The anthers dehisce longitudinally one to four hours after the tepals first unfold. This depends to some extent on ambient temperature and humidity, and anthers dehisce later in wet, cool conditions. Pollen grains are clumped together and pollen remains in the anther thecae until removed by an insect. The three style branches, the distal adaxial surfaces of which comprise the stigmas, are loosely held together for the first three (to five) days that the flower is open and lie laxly over on the dorsal surface of the anthers. On the last day of anthesis, the style elongates and the style branches diverge, arching outward beyond the anthers. At the same time, the conduplicate margins of the distal half of each style branch unfold, exposing the moist, sticky stigmatic surfaces of the now spathulate style branches. Only then are the stigmas of a flower accessible to pollen deposition, and pollen adheres to these areas following hand-pollination.

Thus of the four to six days that a flower is open, it typically has three to five days in an exclusively male phase during which time pollen is usually removed from the anthers by insects. Anthers can be seen with the naked eye to lack pollen after three or four days if flowers were actively visited. By the time the stigma lobes unfold the flower is then in an exclusively female phase that lasts for the final one (or two) days that a flower is open. Mechanical self-pollination cannot readily occur, even if pollen remains in the anthers by the time the receptive stigmatic areas are exposed because of the spatial separation of the pollen-bearing anthers and the stigmatic surfaces. *Gladiolus carmineus*, which we include here as possibly pollinated by large butterflies although we lack pollinator observations, is an exception. The style divides opposite the base of the anthers and the style branches are tangled in the dehisced anthers; thus, selfing could easily occur if there were no incompatibility system (unknown at present). At the *G. carmineus* study site pollen had not been removed from the anthers, and the stigmatic surfaces become dusted with pollen from anthers of the same flower.

Species of *Gladiolus* are medium-sized, cormbearing geophytes, typically 45–120 cm high (Fig. 1A–F). Species pollinated by Lepidoptera typically produce a single, unbranched flowering stem annually. Flowering in a population is synchronous and lasts two to four weeks, and inflorescences are typically secund spikes with the flowers facing to the side and with the floral tube in an ascending position. In *G. nerineoides* the flowers are crowded at the apex of the flowering stem in more or less spiral arrangement and it is the entire inflorescence, rather than individual flowers, that makes for a conspicuous display (Fig. 1B).

Flowers pollinated by moths are moderate in size to large, depending on sectional affinity (Fig. 1C–F). In species of *Gladiolus* sect. *Homoglossum* the perianth tube is mostly 23–60 mm long, but exceptionally 85–110 mm in *G. longicollis* subsp. *platypetalus*. The dorsal tepal, usually slightly larger than the other five tepals, is 32–45 mm long, thus shorter to about as long as the tube (Table 2). In *Gladiolus* sects. *Hebea* and *Linearifolius* flowers are somewhat smaller, and *G. acuminatus* has a floral tube 16–22 mm long and tepals 15–21 mm long. Irrespective of sectional affinity, the perianth tube is more or less cylindric but slightly wider toward the apex, with the slender lower portion 1.5–2 mm in diameter, and fairly straight or gently curved. Flowers are zygomorphic and the slightly larger dorsal tepal is typically inclined while the upper lateral tepals are spread outward. The lower tepals, usually slightly smaller than the upper three, are held loosely together and directed forward. The style and stamens are unilateral and arch to lie close to and just beneath the dorsal tepal and are thus contained within the enclosed space formed by the ascending tepals. The filaments are shortly exserted from the tube, or in *G. longicollis* not or barely exserted, and the anthers lie parallel to one another with the lines of dehiscence facing toward the center of the flower and the lower tepals. In many moth-pollinated *Gladiolus* flowers the tepals are somewhat attenuate with the tips recurved, a feature most exaggerated in *G. acuminatus* and *G. recurvus*.

Moth-pollinated flowers are either shades of white to cream or are lightly to densely mottled with dull purple to brown (Table 2; Fig. 1C–F). Each of the three lower tepals may have a weakly contrasting, darker median band, often collectively referred to as a nectar guide (Goldblatt & Manning, 1998). The bases of the tepals and the distal part of the tube together form a wide throat leading to the narrow, proximal part of the tube. In the sense of Faegri and van der Pijl (1979), these are gullet flowers but often with a particularly elongated floral tube.

A remarkable feature of *Gladiolus liliaceus* is the color shift that occurs at sunset. As the tepals become more fully extended the normally beige, light brown or rusty colored tepals take on a yellowish background hue with the brown pigment changing to light blue-mauve. First reported by Henry Andrews in 1798, this color change has intrigued botanists ever since and is thought to be a direct adaptation to moth pollination (Goldblatt & Manning, 1998). A less pronounced color change at sunset

Figure 1. Comparison of the flowers of southern African *Gladiolus* pollinated by the satyrid butterfly *Aeropetes tulbaghia* (A, B) versus night-flying moths mostly of the families Noctuidae and Sphingidae (C–F), with longitudinal sections of flowers of some species. —A. *G. sempervirens* (sect. *Blandus*). —B. *G. nerineoides* (sect. *Linearifolius*). —C. *G. emiliae* (sect. *Linearifolius*). —D. *G. maculatus* (sect. *Homoglossum*). —E. *G. liliaceus* (sect. *Homoglossum*). —F. *G. guthriei* (sect. *Linearifolius*). Scale bar 10 mm.

also occurs in the related *G. hyalinus*, the tepals of which become paler and more translucent as daylight fades. The darkly mottled tepal coloration may be an adaptation for camouflage, rendering the flowers less visible to nectar or pollen thieves during the day. Johnson (1995) has suggested that the maroon pigmentation of the moth-pollinated flowers of the orchid *Monadenia ophrydea* Lindl. likewise represents camouflage. Moths are believed to locate flowers of this species solely by their scent.

Flowers pollinated by the *Aeropetes* butterfly are fairly large (Table 2), with the exception of *Gladiolus nerineoides*, and have a perianth tube mainly 30–45 mm long, and the dorsal tepal, usually slightly larger than the other five tepals, is mostly 35–65 mm long, thus somewhat longer to about twice as long as the tube. In *G. nerineoides* the somewhat smaller flowers have a floral tube 25–31 mm long and tepals 19–22 mm long, thus shorter than the tube. The perianth tube is more or less cylindric but slightly wider toward the apex, with the slender lower portion 1.5–2 mm in diameter, and fairly straight or gently curved. Flowers are zygomorphic (barely so in *G. nerineoides*) and the larger dorsal tepal either more or less erect, or lightly inclined (*G. cardinalis*), while the upper lateral tepals spread outward. The lower tepals are usually slightly smaller than the upper three and are held loosely together and directed forward. The style and stamens are unilateral and extend outward, and well exserted from the tube. Exceptional *G. nerineoides* has subequal tepals spreading more or less at right angles to the tube and the filaments are included, while the anthers may be partly exserted or entirely included.

Butterfly-pollinated flowers are shades of red, or exceptionally deep pink (*Gladiolus carmineus*), and the lower tepals are often streaked with white. In *G. saundersii* the lower tepals may be almost entirely white with irregular reddish speckling (Table 2). The flowers of all the butterfly-pollinated species lack detectable odor (Table 2). In the sense of Faegri and van der Pijl (1979), these are flag flowers but with a particularly elongated floral tube. The flowers of *G. insolens*, *G. nerineoides*, and *G. stokoei* are uniformly colored.

Nectar analysis (Table 3)

Nectar produced by moth-pollinated species of *Gladiolus* is sucrose-dominant and ranges in concentration from a low of 19.5% (*G. emiliae*) to 36.4% (*G. tristis*) sucrose equivalents. Nectar quantities, measured from unbagged flowers, range from 2.2 to 12.4 μl.

Nectar of butterfly flowers is markedly variable in character, and ranges from sucrose-dominant (*G. cardinalis*, *G. stefaniae*) to sucrose-rich (*G. cruentus*, *G. saundersii*) or hexose-rich (*G. insolens*, *G. nerineoides*) according to the defintion of Baker and Baker (1983). These nectars also have relatively low concentrations, ranging from a low of 18–21% sucrose equivalents in *G. stefaniae* to 26.8% in one of two populations of *G. nerineoides* examined.

Fragrance

Moth-pollinated species of *Gladiolus*, with one exception, produce strong, and often rich sweet odors (Table 4). In species of *Gladiolus* series *Tristis* fragrance is produced at nightfall and is weak or evidently absent during the day. Fragrances vary considerably as perceived by the human nose, though often appear to have a strong clove component and thus resemble the scent of stocks (*Mathiola*) or carnations (*Dianthus*). The odor produced by *G. albens* (sect. *Homoglossum*) is strikingly different, and is somewhat acrid and metallic, while the odor produced by *G. emiliae* (sect. *Linearifolius*) is fruity, with elements of coconut and pineapple. Scent production in *G. hyalinus* is evidently uncommon. In four populations we examined (Die Galg, Gydo Pass, Lion's Head, Nieuwoudtville), all in the west of its geographic range, flowers produced no detectable odor, but collection notes with some herbarium records from the eastern half of its range indicate the presence of a strong, sweet scent. Absence of odor is combined with mottled, brownish or purplish coloration in these populations.

Scent compounds mostly belong to different chemical classes of scents from those of bee-pollinated flowers (Goldblatt et al., 1998a), excepting for linalool, which is present in some bee-pollinated species, notably *G. alatus*, while benzyl acetate is also present in *G. jonquiliodorus*. Scent chemical profiles differ considerably among moth-pollinated species, even though linalool is a common component (Table 4) and is the predominant compound in *G. maculatus*. As in bee-pollinated species of the genus, numerous compounds combine to produce the characteristic scent of each species, and as many as 39 compounds were identified in *G. recurvus* (R. Kaiser, pers. comm.). Surprisingly, *G. acuminatus*, the only species of *Gladiolus* sect. *Hebea* examined, shares no compound with the moth flowers of species of section *Homoglossum* to which belong the other species analyzed. The spicy-clove type scents of *G. liliaceus* and *G. tristis* appear to derive from different compounds, eugenol in the former and eucalyptol in the latter.

Table 3. Available nectar characteristics of species of southern African *Gladiolus* pollinated by Lepidoptera. Nectar analyses were provided by B.-E. van Wyk, Rand Afrikaans University, Johannesburg, South Africa. Number of samples (n) is the same for volume and concentration columns. Data marked with an asterisk (*) are from Johnson and Bond (1994).

Gladiolus species	Nectar volume μl (n)	% Nectar concentration (±SD)	% Range of sugars			Sugar ratio S/F + G (n)
			Fructose	Glucose	Sucrose	
GLADIOLUS* SECTION *BLANDUS						
series *Blandus*						
G. cardinalis	*9.4 (12)	*24.8 (n/a)	9	16	75	3.0 (1)*
G. carmineus	1.7–4.8 (10)	26.1 (3.6)	18	30	52	1.08 (1)*
G. insolens	4.8–7.6 (3)	—	39	38	23	0.26 (1)
G. stefaniae	8.6–11.0 (2)	18–21	10–16	18–25	59–72	1.89 (2)
			*10	12	78	3.5 (1)
GLADIOLUS* SECTION *HEBEA						
series *Permeabilis*						
G. robertsoniae	3.8–4.5 (2)	—	—	—	—	—
GLADIOLUS* SECTION *LINEARIFOLIUS						
series *Linearifolius*						
G. emiliae	3.5–6.6 (3)	22.3 (1.5)	—	—	—	—
	5.7–6.4 (2)	19.5–20.5	8–15	5–9	76–87	4.4 (2)
G. guthriei	4.4–4.8 (5)	31.4 (3.0)	—	—	—	—
G. nerineoides Helderberg	1.8–4.2 (6)	26.8 (2.3)	12–26	23–36	37–63	1.85 (3)
Jonkershoek	2.9–4.6 (3)	23.7 (2.6)	28	46	26	0.35 (1)
GLADIOLUS* SECTION *HOMOGLOSSUM						
series *Gracilis*						
G. albens	3.8–5.6 (4)	27.0 (2.2)	—	—	—	—
G. maculatus	4.8–6.0 (2)	28–30	—	—	—	—
G. recurvus	4.1–13.7 (6)	31.9 (2.0)	6–7	11–14	80–82	4.3 (2)
series *Tristis*						
G. hyalinus Gydo Pass	2.2–4.7 (3)	35.8 (4.8)	2–3	7–8	90	9.0 (2)
Lion's Head	—	—	0–4	2–7	89–98	13.8 (3)
G. liliaceus	3.5–6.4 (5)	35.2 (1.2)	1	2–3	96–97	26.0 (3)
G. longicollis	2.7–3.7 (3)	24.7 (2.5)	6–27	9–23	50–85	2.2 (2)
subsp. *platypetalus*	5.1–7.9 (3)	28.3 (1.5)	6–11	6–11	78–88	4.3 (2)
G. tristis	8.5–12.4 (5)	36.4 (2.1)	—	—	—	—
GLADIOLUS* SECTION *OPHIOLYZA						
G. cruentus	4.8–5.7 (3)	20.7 (2.5)	26.5	39	35.5	0.55 (2)
G. saundersii	14.7–20.1 (5)	24.7	15	42	43	0.75 (1)

POLLINATION MECHANISMS AND POLLEN LOAD ANALYSES

Moth pollination. Observations of pollinators on 7 species of the 11 putatively moth-pollinated southern African *Gladiolus* species showed all of them to be visited by night-flying moths (Table 5). Visitors included sphinx moths alone (*G. longicollis*), sphinx and noctuid moths (*G. emiliae*), or a range of small and larger moths including Noctuidae and other families. No other animals were noted visiting these species either during the day or at night excepting for a single male *Anthophora diversipes* (Apidae: Anthophorinae) captured while attempting to forage for nectar on the long-tubed flowers of *G. recurvus.* Its activities did result in contact of both anthers and stigmatic surfaces, and *Gladiolus* pollen was recovered from its body. This bee should probably not be considered a regular pollinator of the species since the reward offered is not accessible to the bee, which has a tongue up to 12 mm long, while the tube of *G. recurvus* is at least 27 mm long.

Details of moth visits are limited because of the difficulty of observing their activity in the dark or under low intensity red light. Except for species of Sphingidae, moths settled on flowers, grasping the lower tepals, before inserting their probosces into the floral tube (Fig. 2). Too few visits were noted on any species for us to make observations of the duration of visits—we were determined first to capture visiting moths for identification of species and location of sites of pollen deposition. Captured

Table 4. Scent characteristics of selected species of southern African *Gladiolus* with flowers adapted for moth pollination (R. Kaiser, pers. comm.).

Species	Scent description	Scent composition (% constituents above 2%)												
		Benzal-dehyde	Benzyl alcohol	Benzyl acetate or benzoate	Eugenol	Linalool	Methyl benzoate	Eucalyptol	Phenylacet-aldehyde	(E)-ocimene	Epoxy-3, 7-dimentyl 6-octadiene	(E)-ocimene epoxide	(E, E)-alpha farnesene and farnesol	(E)-cinnamic alcohol
G. acuminatus	floral	—	—	—	—	—	—	—	—	31.0	6.2	6.8	7.7	—
G. liliaceus	clove	68.0	—	—	14.1	—	8.1	—	4.0	—	—	—	—	—
G. maculatus	lily	—	—	—	—	91	—	—	—	—	—	—	—	—
G. recurvus	gardenia	—	12.6	6.9	—	69.5	—	—	—	—	—	—	—	5.8
G. tristis	clove	—	—	5.8	3	61.5	10.5	9.5	—	—	—	—	—	—

moths were found to carry *Gladiolus* pollen on the proboscis, but no pollen was recovered from moth bodies. After being netted and transferred to a killing bottle, moths lose many of their body scales and may have also lost any pollen they might have carried. Nevertheless, those moths with elongate probosces, including the sphingids *Hippotion* and *Agrius* and the noctuid *Cucullia*, must be regarded as legitimate pollinators of the species on which they were captured. Moths in the families Archiidae and Geometridae with shorter probosces, 10 mm long or less, that were also captured, cannot reach nectar in the floral tubes and must be regarded as accidental visitors, perhaps attracted by the strong floral odors.

Butterfly pollination. Five species (Table 5) were seen to be visited by *Aeropetes tulbaghia* and another four species (*Gladiolus carmineus*, *G. cruentus*, *G. insolens*, and *G. stokoei*) have similar flowers and are inferred to share this pollination strategy. This large butterfly has a wingspan of ca. 80 mm, a large body ca. 20 mm long, and a proboscis 28–34 mm long (Johnson & Bond, 1994; Johnson, 1994). *Aeropetes* was seen fluttering around flowers of *G. cardinalis*, *G. nerineoides*, *G. saundersii*, *G. sempervirens*, and *G. stefaniae* (spanning three sections, *Blandus*, *Linearifolius*, and *Ophiolyza*, Table 5), sometimes settling for 25 to 130 seconds, and then to fly to other flowers of the same species. As Johnson and Bond (1994) have noted, the behavior of butterflies included inspection visits when individuals flutter above flowers without settling or feeding. During such visits, the ventral part of the thorax, abdomen, and wings may brush against the well-exserted anthers or stigmatic surfaces of species like *G. cardinalis*, *G. sempervirens*, and *G. stefaniae* (sect. *Blandus*). Pollen and stigmatic surfaces of *G. nerineoides* (sect. *Linearifolius*) and *G. saundersii* (sect. *Ophiolyza*) are only contacted during feeding visits when insects settle, grasping the tepals and inserting their proboscis into the perianth tube. In *G. nerineoides* pollen is deposited only on the upper proboscis because the anthers are not or are only shortly exserted from the floral tube. Pollen is deposited on the head, antennae, and dorsal part of the thorax of *G. saundersii* because the hooded dorsal tepal, under which the anthers lie, forces a feeding insect to orient its body nearly vertically as it grasps the upper lateral or lower tepals. No other animals were ever seen visiting those *Gladiolus* species that attracted *Aeropetes*, and this single insect must be assumed to be their sole pollinator.

The innate attraction that *Aeropetes* exhibits for red flowers, particularly those of large size, or col-

Table 5. Length of perianth tube of *Gladiolus* species (from Goldblatt & Manning, 1998, representing the ranges for the species, measured from all known herbarium collections) and mouthparts of captured moths. Few butterflies were captured because their identity is not in question; the few individuals captured were released after sites of pollen deposition were noted because *Aeropetes* is a legally protected species. Family affiliations: Archiidae: *Hypagoptera*; Geometridae: *Macaria*: Noctuidae: *Cucullia, Syngrapha, Tychopmoptes*; Satyridae: *Aeropetes*; Sphingidae: *Agrius, Hippotion*. Note: the "spurge hawkmoth" reported on *G. longicollis* by J. M. Wood (in Scott Elliot, 1891) may also have been *A. convoluli*.

Plant species	Perianth tube (mm)	Lepidopteran species (n)	Mouthpart (mm)	Position of pollen on insect body
GLADIOLUS* SECTION *OPHIOLYZA				
G. saundersii	33–37	*Aeropetes tulbaghia*	not measured	frons, dorsal thorax
GLADIOLUS* SECTION *BLANDUS				
G. cardinalis	30–45	*Aeropetes tulbaghia*	not captured	not available
G. sempervirens	30–45	*Aeropetes tulbaghia*	not captured	not available
G. stefaniae	44–55	*Aeropetes tulbaghia*	not captured	not available
GLADIOLUS* SECTION *LINEARIFOLIUS				
G. guthriei	16–18	*Cucullia inaequalis* (1)	ca. 16	distal 12 mm of proboscis
G. emiliae	32–45	*Hippotion celerio* (1)	ca. 30	distal 25 mm of proboscis
		Cucullia inaequalis (1)	ca. 28	distal 25 mm of proboscis
		Cucullia extricata (1)	ca. 20	distal 15 mm of proboscis
		Macaria simplicilinea (1)	<10	no pollen
		Hypagoptera sp. (1)	<10	no pollen
G. nerineoides	16–18	*Aeropetes tulbaghia*	not captured	not available
GLADIOLUS* SECTION *HOMOGLOSSUM				
G. liliaceus	40–45	*Cucullia extricata* (1)	ca. 28	distal 25 mm of proboscis
G. longicollis	85–110	*Agrius convolvuli* (1)	110–115	25 mm from base of proboscis
G. maculatus	23–35	*Cucullia terensis* (1)	25–30	distal 25 mm of proboscis
		Cucullia sp. (1)	15–20	from base of proboscis
G. recurvus	27–36	*Hippotion eson* (1)	ca. 40	distal 25 mm of proboscis
G. tristis	40–60	*Syngrapha circumflexa* (3)	16–17	dorsal thorax and proboscis
		Tychomoptes inferior (1)	ca. 10	no pollen

lectively making a prominent display, as in *G. nerineoides*, is well known and has been documented elsewhere (Johnson & Bond, 1994; Goldblatt et al., 1999). The wavelength range of red color exhibited by *Aeropetes* flowers is virtually the same as that in red-flowered species pollinated by sunbirds. There is no evidence of effective pollination of the butterfly-pollinated species of *Gladiolus* by sunbirds as there is, for example, in red, tubular-flowered species of *Tritoniopsis* and *Watsonia* (Iridaceae), *Kniphofia* (Asphodelaceae), and *Erica* (Ericaceae), which may use both sunbirds and *Aeropetes* equally as pollinators (Johnson & Bond, 1994; Goldblatt et al., 1999). Possibly the inclined, and somewhat flaccid stem and difficulty in reaching the perianth tube because of the large, widespread tepals discourage sunbird visits. In connection with *Aeropetes* pollination, the record of this butterfly on *G. cruentus* (Johnson & Bond, 1994) must be mentioned. From the locality (J. J. Vlok, pers. comm.) this is clearly for the high-altitude Drakensberg species, *G. flanaganii*, and probably reflects the innate attraction to red color by *Aeropetes*. The very fleshy, stiff cupped tepals, sturdy flowering stem, and hooded dorsal tepal of this species (Goldblatt & Manning, 1998) are suited to sunbird pollination but seem unsuited to butterfly pollination, as does the nectar, which has a concentration of 35% sucrose equivalents (Goldblatt et al., 1999). The report of the *Nectarinia famosa* visiting *G. flanaganii* is consistent with the floral adaptations of the species, and *Aeropetes* may simply have been a casual visitor. *Gladiolus cruentus* is restricted to lower elevations inland from the central KwaZulu–Natal coast (Goldblatt & Manning, 1998) where *Aeropetes* is rare or normally absent, and this red-flowered species may be pollinated by alternative large butterflies, such as *Papilio demodocus* and *P. nereis*, as has been found for lower-elevation populations of another red-flowered species of Iridaceae, *Hesperantha coccinea* (Backh. & Harv.) Goldblatt & J. C. Manning (Goldblatt et al., in press).

Discussion

Although aspects of pollination of *Gladiolus* species by moths and the satyrid butterfly *Aeropetes*

Figure 2. Noctuid moths photographed while visiting flowers of *Gladiolus.*—A. *Cucullia extricata* on *G. liliaceus.*—B. *Cucullia* cf. *terensis* on *G. maculatus* (this particular moth was not captured).

have already been documented (Johnson & Bond, 1994) or discussed in more general terms (Goldblatt & Manning, 1998; Goldblatt et al., 2001), these two quite different pollination systems are more fully documented here. Moreover, comparison of moth- or butterfly-pollinated species with their closest relatives with different pollination systems makes it possible for us to draw reasonable conclusions about the evolution of both pollination systems in the genus, for which a hypothetical phylogeny already exists (Goldblatt & Manning, 1998). Moth pollination (Table 6) has evolved in three sec-

Table 6. Analysis of the frequency and taxonomic distribution of night-flying moth and butterfly pollination systems in southern African species of *Gladiolus.* Numbers in parentheses in columns 2 to 5 represent number of species inferred to have the pollination system.

Pollination system	Section					Total species confirmed	Taxonomic sections (series)	Total confirmed and inferred
	Ophiolyza	*Blandus*	*Linearifolius*	*Hebea*	*Homoglossum*			
Moth	0	0	2 (0)	0 (2)	5 (2)	7	3 (5)	11 (7%)
Large butterfly	1 (1)	3 (2)	1 (1)	0	0	5	3 (3)	9 (5%)

tions of *Gladiolus, Hebea, Homoglossum,* and *Linearifolius,* while butterfly pollination evolved in *Gladiolus* sects. *Blandus, Ophiolyza,* and *Linearifolius.* Within section *Hebea* the two moth-pollinated species, *G. acuminatus* and *G. robertsoniae,* have such different flowers that we do not believe they are immediately related. More likely they evolved from different, bee-pollinated ancestors. Similarly, the moth-pollinated species of section *Homoglossum* belong in different series (Tables 1, 2). In addition, in series *Gracilis* both floral and leaf morphological differences between *G. recurvus,* which has apomorphic leaves with winged margins, like those of *G. gracilis* Jacq., and *G. albens* and *G. maculatus,* which have leathery leaves without prominent margins or midribs, suggest that *G. recurvus* is not immediately related to the latter species pair. Lastly, in *Gladiolus* sect. *Linearifolius,* the only section with both moth- and butterfly-pollinated species, species with the two pollination systems fall in different lineages (Goldblatt & Manning, 1998).

These considerations led to the hypothesis that moth pollination arose six times within the southern African species of *Gladiolus* while butterfly pollination arose at least three times (Table 6). Comparison of the pollination systems of immediate ancestors of moth- or butterfly-pollinated species makes it likely that moth pollination arose from bee-pollinated ancestors in *Gladiolus* sects. *Hebea* and *Linearifolius,* and in series *Gracilis* of section *Homoglossum.* The sister clade of series *Tristis,* series *Homoglossum,* comprises only bird-pollinated species, but we cannot say whether the predominantly moth-pollinated series *Tristis* evolved from bird-pollinated ancestors or the putative common ancestor of the two series, series *Teretifolius,* which comprises mostly bee-pollinated species (Goldblatt & Manning, 1998; Goldblatt et al., 1998a). In tropical Africa, *Gladiolus* sect. *Acidanthera,* with seven species, also shows all of the classic adaptations for moth pollination. The perianth is white and the perianth tube 60–150 mm long depending on the species (Goldblatt, 1996), and flowers produce a strong odor that, at least for the widely cultivated *G. murielae* Kelway (= *G. abyssinicus* (Brongn. ex Lemaire) Goldblatt), is strongest at night (unpublished obs.). The flowers of two species of the section, *G. aequinoctialis* Herbert and *G. murielae,* are unusual for moth pollination in having dark blotches on the lower tepals, and the entire section *Acidanthera* has an unusual specialization, anthers with stiff, acute apical appendages (Goldblatt, 1996). Because of the length of the perianth tube in species of section *Acidanthera,* mostly 90–140 mm long, pollination by sphinx moths (Sphingidae), which have probosces of comparable length, is inferred but there are no pollination studies for the *Gladiolus* species of tropical Africa.

One notable aspect of the evolution of moth pollination in the three southern African sections of the genus in which it occurs is that these sections (*Gladiolus* sects. *Hebea, Homoglossum,* and *Linearifolius*) are the only ones in which floral fragrance is well developed (and is associated primarily with bee pollination). As we have noted elsewhere (Goldblatt et al., 1998a), floral fragrance is common in the southern African species of the winter-rainfall zone where sections *Hebea* and *Homoglossum* are best represented. It is also present in a few summer-rainfall zone species of the above sections that have their closest allies in the winter-rainfall zone. The scarcity of moth-pollinated species in summer-rainfall parts of southern Africa may be the result of the absence of scent in sections of the genus centered there. In tropical Africa scent in moth-pollinated species of section *Acidanthera* appears to have evolved independently within the section (the section as currently defined does not occur in southern Africa). Floral odor in *Gladiolus* species (Goldblatt et al., 1998a) is the result of the combination of many substances and in moth flowers perceived odor represents different mixes and proportions of these same series of compounds.

Apart from fragrance, moth flowers differ from their bee-pollinated ancestors in perianth tube length, color, and size of the tepals. Large size is probably important for display purposes at night as is the pale coloration. An unusual aspect of moth-pollinated flowers in *Gladiolus* is the frequency of dull patterning or mottling on a pale background, most notable in *G. hyalinus, G. liliaceus, G. maculatus,* and even some forms of *G. longicollis* (all sect. *Homoglossum*) and in *G. emiliae* and *G. guthriei* (sect. *Linearifolius*). Dark mottling is less pronounced in *G. hyalinus* and *G. liliaceus* at night, as the pigments either change in intensity or color or both. The mottling may be camouflage, protecting flowers from predation during the day, as Johnson (1994) has suggested for the maroon-flowered orchid, *Monadenia ophyridea,* which is presumably located by its settling moth pollinators by scent alone.

Butterfly-pollinated flowers in *Gladiolus* sect. *Blandus* appear to have evolved from ancestors adapted for pollination by long-proboscid flies, the predominant pollination system in the section, and the one present in species most closely allied to the clade of butterfly-pollinated species in the section (Goldblatt & Manning, 1998, 1999). Long-probos-

cid fly flowers have similarly long floral tubes and differ most significantly in floral pigmentation, cream or pink with red nectar guides often outlining a white zone. In *Gladiolus* sect. *Ophiolyza* the ancestors of the two butterfly-pollinated species have flowers adapted for pollination by sunbirds (the *G. dalenii* complex) (Goldblatt et al., 1999). In series *Linearifolius* butterfly-pollinated *G. nerineoides* and *G. stokoei* (putatively butterfly pollinated) fall within a clade with the bee-pollinated *G. brevifolius* and long-proboscid fly pollinated *G. monticola* (Goldblatt & Manning, 1998, 1999).

At first it might appear that a simple shift from ancestral pink or cream flowers to red ones may effect a shift to butterfly pollination. In *Gladiolus* increase in flower size appears equally important. Moreover, other more subtle changes suggest that more complex genetic adaptations are necessary, including a shift in the position of the anthers and stigmatic surfaces, either prominently exserted or included in the floral tube, and a shift in flowering time (butterflies are on the wing only in late summer). In the winter-rainfall zone a whole series of vegetative and physiological adaptations would also be required to produce flowers in an area of summer heat, drought, and low atmospheric humidity, a time that necessitates the separation of vegetative growth from the flowering phase of the life cycle.

Johnson and Bond (1994) have pointed out a feature of butterfly pollination in the southern African winter-rainfall zone that relates directly to this question. This is that so many butterfly-pollinated species of the area are rare, or are highly local endemics. We suspect this has nothing to do with the intrinsic effects of having a specialist pollination system and is correlated instead with the fact that species flowering in the late summer and autumn in an area of mostly winter precipitation require highly specialized habitats that are by their very nature highly local. Thus, *G. cardinalis* survives summer drought by growing along watercourses in cool mountain habitats, often in the spray of perennial waterfalls. *Gladiolus sempervirens*, *G. stefaniae*, and *G. stokoei* also grow in montane habitats and are restricted to slopes with poor drainage where the summer southeast winds bring moisture in the form of fog that keeps the ground moist at this otherwise dry season. *Gladiolus nerineoides* is restricted to shaded south-facing cliffs where moisture percolating from the slopes above keeps their substrate relatively damp. Even in these specialized habitats vegetative specialization makes survival for these summer-flowering species possible. *Gladiolus nerineoides*, *G. stefaniae*, and *G. stokoei* produce foliage leaves in the winter, after the wet season has begun. Their flowering stems bear short, often entirely sheathing, and sometimes dry leaves while the foliage leaves are dry and often lost by the time flowers are produced.

An aspect of evolution of specialized pollination systems is a change in the nature of the reward. Bee-pollinated species of *Gladiolus* mostly produce sucrose-rich or sucrose-dominant nectar of relatively high concentration (Goldblatt et al., 1998a). The pattern in moth-pollinated flowers is similar, although sugar concentration is often higher. This pattern is one that is common in the Iridaceae. In moth-pollinated species of *Hesperantha* (Goldblatt et al., in press) nectar sugars usually have concentrations of 45–50% sucrose equivalents. The relatively high volume of nectar in most moth flowers, especially compared to their presumed bee-pollinated ancestors, may relate to the higher nutrient needs of active, fast moving moths with relatively large bodies, especially in the case of Sphingidae, which hover while feeding.

Unlike nectar of moth flowers, the nectar of butterfly-pollinated *Gladiolus* species shows a lower sugar concentration than their presumed long-proboscid fly or bee-pollinated ancestors (Goldblatt et al., 1998a; Goldblatt & Manning, 1999), but a relatively high volume. Exactly why the lower nectar sugar concentration is characteristic of large butterfly pollination is uncertain. The higher viscosity of concentrated nectar may make it difficult for an insect to draw through the proboscis, but this is evidently not a consideration for small or large moths, which have similarly constructed and sometimes equally long and narrow mouthparts. Another feature of butterfly nectars in *Gladiolus* is the shift to higher proportions of hexose sugars. While most species of section *Blandus* have the sucrose-dominant type nectar found in related long-proboscid fly pollinated species (Goldblatt & Manning, 1999), *G. insolens* has hexose-rich nectar. A similar but less pronounced shift is evident in the two butterfly-pollinated species of section *Ophiolyza*, which have sucrose-rich nectar with nearly equal proportions of sucrose and hexose sugars, and in *G. nerineoides*, which shows the same shift, while related species have nectar with higher proportions of sucrose (Goldblatt & Manning, 1999; Goldblatt et al., 1999). Such changes in nectar sugar chemistry are rare in the Iridaceae, especially in the subfamily Crocoideae (syn. Ixioideae) to which *Gladiolus* belongs, and are presumably pollinator driven, reflecting a preference of *Aeropetes* for nectar with elevated levels of hexose sugars, rather than a random change.

Shifts in pollinators are common within the larg-

er genera of the African Iridaceae and are an important factor in the radiation of the family. Elsewhere we have speculated that as many as 32 shifts in pollination system have occurred just in *Gladiolus* in southern Africa (Goldblatt et al., 2001). This represents an average of one shift for every five species. The convergent evolution of moth pollination at least six times and butterfly pollination three times reflects the evolutionarily labile floral and vegetative morphology of this highly successful genus. As outlined above, shifts that may appear quite simple, appearing to represent changes mainly in pigmentation and floral tube length are, in fact, complex and represent a closely integrated series of adaptations that include, in addition to floral patterning, shifts in fragrance characteristics, timing of the opening and closing of the tepals and sometimes scent release, nectar physiology, seasonal phenology, and associated vegetative adaptations for those species of the southern African winter-rainfall zone that flower in summer. The developmental complexity associated with these shifts makes their high frequency seem even more impressive.

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INTRODUCTION: CONSERVATION AND THE FUTURE OF LIFE[1]

George E. Schatz[2] *and P. Mick Richardson*[2]

Upon initial thought, conservation might seem an anomalous topic for a systematics symposium. However, although systematics is often perceived only in its arcane, classificatory function, and conservation has primarily had a public persona of dwindling populations of charismatic large animals, they are in fact two sides of the same coin. Or said another way, they concern themselves with a common currency, i.e., the diversity of life on Earth. Indeed, one of the goals of the 47th Annual Systematics Symposium was to highlight the intimate connection between systematics and conservation. As scientific disciplines, both encompass broad approaches, from the "top-down" landscape and ecoregion paradigms of conservation, and the "Tree of Life" phylogenetic perspective in systematics, to "bottom-up" Population Viability Analyses and ex situ interventions in conservation, and analyses of genetic variability in systematics. At all levels, systematics directly informs conservation, and all perspectives ultimately converge upon species, the most recognizable unit of biodiversity.

Among the countless species in the cornucopia of biodiversity, one species—our own—has distinguished itself from all others. Human beings have the dubious distinction of having become the most successful species of all time. In achieving that success, we have become the first species to alter basic biosphere processes since the original photosynthetic bacteria added oxygen to the atmosphere and sent evolution down an aerobic path. Although the rise of one species has undoubtedly often contributed to the decline of another species during that long evolutionary continuum, our success now directly or indirectly negatively impacts (or eventually will impact) nearly all of the other 10–100 million species with whom we share our home. We are both the problem, and the only potential solution.

But as E. O. Wilson (2002) so eloquently articulates in his most recent book, *The Future of Life*, there is much about which to be hopeful in the urgent search for solutions. The following Symposium contributions all embrace that optimism, illustrating the full range of "top-down" to "bottom-up," ultimately human-centered approaches. Joel Cracraft invokes the renaissance in systematics during the past several decades and its ensuing di-

[1] This and the six articles that follow it constitute the proceedings of the 47th Annual Systematics Symposium of the Missouri Botanical Garden. The symposium was held in St. Louis, Missouri, 13–14 October 2000. The symposium was supported in part by the National Science Foundation under grant DEB-9981642. PMR thanks Peter Raven for helping to select a fine diversity of speakers, Kathy Hurlbert and her expert staff for organization and administration skills, John Myers for his illustration used on the cover of the symposium brochure, Victoria Hollowell, Amy McPherson, and Diana Gunter for their editing and political skills, and the speakers for being such an interesting group of scientists.
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rect application to societal problems as evidence of its relevance in conserving and sustainably using biodiversity. Both he and George Schatz emphasize the fundamental importance of the natural history collections that underpin all our knowledge of biodiversity, and underline their critical role in directly informing conservation planning using powerful new informatics tools. The mapping of biodiversity shows us that most species are not randomly distributed over the face of the earth, and that collectively they form distinct associations, often highly restricted in area, that correlate with the variety of life-supporting milieu and historical phenomena of isolation and dispersal. Thus, David Olson and Eric Dinerstein advocate the landscape paradigm to ensure functional representatives of each of the world's distinct ecoregions, i.e., those that satisfy the minimum size requirements of all their constituent species, and retain the potential for migratory processes.

In virtually all of those ecoregions, we are one of the constituent species, often the dominant one; for better or, now, mostly worse, all of the rest of the species are consigned to live alongside us. Again, we are the only potential solution. Gary Nabhan and his colleagues paint a portrait of the Colorado Plateau in which indigenous cultural diversity and biological diversity reciprocally sustain one another, serving as an example for the local, community-based management of biodiversity. Debra Moskovits and her colleagues present an inspiring vision of Chicago Wilderness that serves to resurrect our innate capacity for stewardship amidst even our most dense, urban environments. In contrast, Stuart Pimm validates the alternative scenario, dispelling once and for all any lingering myths that we are not the current agents of extinction, which indeed we regrettably are.

The consequences of our success, and the ultimately self-detrimental manner in which we currently live, are becoming increasingly clear. As we strive to disseminate our emerging knowledge, we must nurture the belief that it will soon foster the ethical principles and moral standards by which we will fully embrace not only each other, but all of our fellow species.

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THE SEVEN GREAT QUESTIONS OF SYSTEMATIC BIOLOGY: AN ESSENTIAL FOUNDATION FOR CONSERVATION AND THE SUSTAINABLE USE OF BIODIVERSITY[1]

Joel Cracraft[2]

Abstract

The three missions of Systematics Agenda 2000 (SA2000)—to inventory Earth's species, to understand their relationships, and to use the latter to create predictive information systems—define an agenda of research for systematic biology. The recognition that systematic knowledge underpins biological knowledge in general, and applied biology in particular, has resulted in an amazing growth in systematics over the past decade. Increasingly, systematics is being used to solve societal problems. This paper describes seven great questions within systematics and discusses their relevance for, and contribution to, conserving and sustainably using biodiversity. These questions fall into four broad categories: *Questions about diversity*: What is a species? and How many species are there? *Questions about phylogeny*: What is the Tree of Life? and What has been the history of character transformation? *Questions about biogeography*: Where are Earth's species distributed? and How have species' distributions changed over time? and *Questions about phyloinformatics*: How is phylogenetic history predictive?

Key words: biogeography, diversity, inventory, phylogenetics, phyloinformatics, systematics, Systematics Agenda 2000.

Systematic biology occupies the central core of biodiversity science. The four great themes of systematics—diversity, phylogeny, biogeography, and classification (to be subsumed here into a broader context termed phyloinformatics)—form a critical foundation for all other disciplines of biology. The discovery and naming of life's diversity, its evolutionary history, its distribution across Earth to form habitats and ecosystems, as well as how comparative information about organisms can be organized in a predictive manner, underpin, to one degree or another, all biological knowledge.

Beginning in the early 1990s systematists became increasingly engaged in conservation and the role played by systematics in solving societal problems (Systematics Agenda 2000, 1994a, 1994b). Since then, systematists have published numerous papers that address the contributions of systematics to conservation biology, focusing especially on such topics as diversity patterns, species concepts, geographic distribution, and endemism. The recognition of the importance of systematics has never been stronger.

There is a sense, however, in which some of these discussions linking systematics and conservation can be said to be too narrow, both from the perspective of systematics and from conservation. Thus, "conservation," at least in the expansive sense it will be used here, is more than just efforts to save endangered species and ecosystems, or to create protected areas. While certainly embracing these objectives, conservation in the real world covers much more ground philosophically, as well as in practice. In a world losing its biodiversity at an accelerating rate, systematics needs to be seen as a crucially relevant and important science in meeting the challenges of global environmental change (sensu lato), at the same time contributing strongly to traditional conservation practice.

It will therefore be a theme of this paper that systematics and systematists should be approaching conservation as a subset of solutions that must be

[1] I thank Peter Raven and P. Mick Richardson for asking me to participate in the 47th Annual Systematics Symposium at the Missouri Botanical Garden. Meredith Lane made many helpful comments on the manuscript that greatly improved its clarity; I am most grateful to her. Many of the intellectual seeds of this article derive from the hard work and brilliance of the hundreds of systematists who contributed to Systematics Agenda 2000, which started in the United States but has now spread worldwide. The initial effort of Systematics Agenda 2000 was supported by a grant from the U. S. National Science Foundation (DEB-9396035). Consider this yet another contribution from that investment.

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implemented to mitigate the adverse effects of environmental impacts in general, all the time realizing that the contributions undertaken to sustain and improve human well-being can themselves be seen as a conservation initiative. Stemming the loss of biodiversity is essential, but the factors leading to that loss are imbedded in a complex causal nexus that encompasses all aspects of society. People across the globe use tens of thousands of species to sustain their lives in one way or the other, and the causal complexity of that use is what makes saving biodiversity so difficult—it cannot be separated from how societies function. This reality is encapsulated in the activities of the Convention on Biological Diversity (CBD) and many nongovernmental organizations. Effective conservation efforts cannot be separated from the elimination of poverty, which cannot be separated from the improvement of women's health, education, and economic enfranchisement, which cannot be disentangled from governmental policies of many kinds, and on and on. New knowledge about the world (science) is necessary to meet the many environmental challenges created by human activities, and thus systematics can help in all sorts of ways not generally realized by most practicing systematists or other biodiversity scientists. This is what I mean by the need for systematists to have a more expansive vision for their discipline and for its importance.

This paper explores the contributions of systematics to science and society, firstly, by summarizing some of the literature published since the mid-1990s, when participants in Systematics Agenda 2000 (SA2000) released many of their assessments, and secondly, by pointing to new developments that will become increasingly important in the future. This will be done within the framework of what might be called the seven great questions of systematic biology, which to me at least, encapsulate most of the research agenda, and importance, of systematics to society. Not all of these questions will be treated equally here, inasmuch as some have been the subject of a substantial recent literature (see citations below).

Systematics Agenda 2000: Bringing Systematics to Society

In the early 1990s the Society of Systematic Biologists, the American Society of Plant Taxonomists, and the Willi Hennig Society, in cooperation with the Association of Systematics Collections, launched an effort to document the importance of systematics to society (Anonymous, 1991). Through its many publications, Systematics Agenda 2000 transformed the way systematists view their own discipline, and it helped create an atmosphere in many countries throughout the world in which systematics gained in stature and importance as an integral component of biodiversity science.

Because many systematists, both young and old, might be unfamiliar with the rich panoply of published results of this effort, these are summarized in Table 1. These papers cover a broad range of subjects that articulate the importance of systematics. Collectively, they have reached out to systematists and biodiversity science policymakers around the world and have been responsible, in varying degrees, to promoting and building systematics. Thus, to take one example, following SA2000 symposia at the Royal Society in London (Claridge, 1995) and the French Academy of Sciences in Paris, new initiatives were formed to promote the objectives of systematics across Europe (Blackmore & Cutler, 1996).

Systematics Agenda 2000, although begun in North America, was developed as a global effort. Thus, the core documents of SA2000 were intentionally not copyrighted so that they could be taken, and used, by systematists to promote systematics research and capacity building anywhere. Translations were encouraged, and that strategy worked as numerous individuals and groups adopted the language and content of SA2000 in their efforts (Table 1). Today, SA2000 is truly international. Systematics Agenda 2000 International (SA2000I) is a program of the International Union of Biological Sciences (IUBS) and functions as the systematics core element of the international biodiversity science program DIVERSITAS [DIVERSITAS]. Through DIVERSITAS, SA2000I has been active in providing advice on systematics science and capacity building to the Convention on Biological Diversity (CBD) and its Global Taxonomy Initiative [GTI]. Some of the SA2000I/DIVERSITAS documents in support of the GTI are available on the CBD website; these documents contain recommendations that have been adopted by the CBD Conference of the Parties (the 181 countries that have ratified the Convention). (For the record, as of 12 September 2001, only six signatory countries to the CBD have failed to ratify: Afghanistan, Yugoslavia, Thailand, Tuvalu, Kuwait, and the United States of America.)

The Seven Great Questions of Systematics

The scientific agenda of systematics and its relevance for society occupy four great themes: diversity, phylogenetic history, biogeography, and clas-

Table 1. An overview of the papers produced by participants in Systematics Agenda 2000 over the last decade. These publications treat the role and importance of systematics to society, discuss aspects of building systematics science capacity, or address policy issues involving systematics and biodiversity.

Publication	Theme
General SA2000 Documents	
Anonymous (1991)	Announced formation of SA2000
Systematics Agenda 2000 (1994a)	Color brochure discussing importance of systematics and describing SA2000's three missions
Systematics Agenda 2000 (1994b)	Technical report providing detail for 1994a
BioScience 1995 (vol. 45, no. 10)	
Simpson & Cracraft (1995)	Overview of systematics and papers in *BioScience*
Savage (1995)	Role of systematics in biodiversity science
Miller & Rossman (1995)	Role of systematics in agriculture
Brooks et al. (1995)	Role of systematics in ecology and behavior
Lauder et al. (1995)	Role of systematics in comparative morphology and physiology
Davis (1995)	Systematics and public health
Biodiversity and Conservation 1995 (vol. 4, no. 5)	
Claridge (1995)	Introduction to SA2000 symposium held at the Royal Society, 12 April 1994
Eshbaugh (1995)	Overview and history of SA2000
Cracraft (1995)	Building systematics and biodiversity science capacity
Wheeler (1995a)	Biodiversity and systematics inventories
Prance (1995)	Systematics, conservation, and sustainable development
Jones (1995)	BioNet-International and capacity building
McNeely (1995)	Systematics and conservation
Annals of the Missouri Botanical Garden 1996 (vol. 83, no. 1)	
Richardson (1996)	Introduction to SA2000 Symposium, 41st Annual Systematics Symposium, MOBOT
Monson (1996)	Phylogenetics and comparative plant physiology and development
Rossman & Miller (1996)	Role of systematics in agriculture and forestry
Vecchione & Collette (1996)	Role of systematics in fisheries and marine biodiversity
Oliver (1996)	Importance of systematics for public health
Vane-Wright (1996)	Role of systematics in conservation
Balick (1996)	Systematics and ethnobotany
Other publications	
Systématique Agenda 2000 (1994)	French translation of SA2000 (1994a)
Wheeler (1995b)	Systematics and biodiversity policy
Agenda Systematik 2000 (1996)	German translation and expansion of SA2000 (1994b)
Blackmore & Cutler (1996)	Building SA2000 in Europe
Wheeler & Cracraft (1996)	Building systematics capacity
American Museum of Natural History (1999)	Workshop report, cosponsored by SA2000 International, on Convention of Biological Diversity Global Taxonomy Initiative
Baas (1999)	SA2000I, DIVERSITAS, and the CBD
Cracraft (2000)	Building systematics capacity

sification. Each of these four themes leads to a series of fundamental questions—the seven great questions of systematics. These questions broadly cover what systematists do, and are why, in my opinion, systematics is the central, undeniable core of biodiversity science.

THE FIRST GREAT QUESTION: WHAT IS A SPECIES?

No question, probably, has generated more controversy, been so opaque to solution, and yet remains as crucial and important today as it ever has, than "What is a species?" In systematics, which is

a taxon-based science, it is unquestionably the most fundamental question that can be asked. Astonishingly, many biologists profess to be tired of the controversies over this question, yet instantly remain willing to engage in the debate, whether or not they themselves are professionally concerned with individuating species limits, i.e., whether they are systematists or not. Everyone, it seems, knows what a species is, or more likely, what is not!

The reason for the dispute is fairly obvious: at some level, notions of species are at the very heart of biological understanding and so there is a lot at stake. Species concepts intersect with a whole series of conceptual and disciplinary agendas, from those of systematists who discover and describe Earth's diversity, to those reconstructing phylogeny and biogeography, to those attempting to understand the origins of species from a genetic or ecological viewpoint, to those interested in conservation, ecology, and applied biology. Species are the basic units of systematics, evolutionary biology, and diversity. Thus, species concepts touch upon elemental philosophical arguments about the reality of the units of nature as perceived by biologists of varying disciplines as well as scientific opinion about how life evolves.

Given this crucial importance, it is ironic that there is so much divisiveness over "What is a species?" You would think biologists could have solved this issue by now. Yet each year brings forth numerous papers on the subject, and books keep flowing (most recently, for example, Ereshefsky, 1992; Kimbel & Martin, 1993; Claridge et al., 1997; Howard & Berlocher, 1998; Wilson, 1999; Wheeler & Meier, 2000), all with no diminution of differences of opinion.

Nevertheless, it can be argued that over the last decade, practicing systematists—those biodiversity scientists whose research most directly bears on this issue—are gradually converging upon a common solution to this question, either as a result of practical or theoretical considerations, or both. These systematists see species as basal (smallest) clusters of diagnosably distinct populations (groups of individual organisms). Most of these systematists do not endorse a particular concept of species; they go about their work inventorying, describing, and monographing without a heavy burden of theorizing. But if one had to put a name on their concept, it would appear to be most similar to that advocated by supporters of a phylogenetic species concept (Nelson & Platnick, 1981; Cracraft, 1983, 1989a; Nixon & Wheeler, 1990; Wheeler & Platnick, 2000).

The reason why this is the most common approach to species is very practical, as well as simply a matter of numbers: the majority of systematists working on invertebrates, especially insects, many plant groups, and various vertebrate taxa view species as basal diagnosable units because this best fits the way they partition the taxonomic variation they have observed. How could this not be the case when the large majority of described species are known from a handful of specimens, often single individuals? Or when nothing is known about their biology or patterns of genetic variation?

Thus, the debate over species, in a practical sense, comes down to a choice between a phylogenetic species concept (PSC) and a biological species concept (BSC). The latter, surprisingly, is applied by very few practicing systematists who inventory and describe species, but has strong support from advocates of the evolutionary systematics of Mayr (1942, 1963, 1982, 2000) and by those whose interests lie with population genetics (Coyne et al., 1988; Avise & Ball, 1990) or evolutionary biology in general (e.g., Bock, 1987; Futuyma, 1998). The interchanges among advocates of the PSC and BSC have been incessant. It is not my purpose to review these debates as the central arguments and positions can be found in Wheeler and Meier (2000). Instead, pursuant to the theme of this paper, I comment briefly on the relevance of species concepts to conservation and applied biology.

Species concepts are important because they allow us to propose hypotheses about the ontology of nature: different species concepts generally imply a different ontology (Cracraft, 1987, 1989b). This is not just philosophical mumbo-jumbo. One needs a clear idea of the entities of nature so that one can count and describe patterns of diversity, as well as understand how entities behave (i.e., how they participate in processes). Thus, there are very practical consequences stemming from the adoption of a particular species concept, especially in the description and enumeration of diversity.

Conservation biology, although inherently cross-disciplinary, emerged primarily from an ecological tradition, and ecologists and other non-systematist biodiversity scientists have come to their understanding of species and speciation through their formal university training in ecology, genetics, and evolution. Most of that training has accepted the BSC because it has been the canonical view of species since the early influential work of Ernst Mayr (1942, 1963) and because it has been followed in most contemporary textbooks (e.g., Futuyma, 1998). However, many conservation biologists began to see a problem with applying the BSC because of its

ambiguous treatment of discrete taxonomic variation. Thus, under the BSC, diagnosable populations might be ranked either as a species or subspecies, or subspecific rank itself might be applied to diagnosably distinct forms as well as to arbitrary subdivisions of clinal variation.

In an influential paper, Ryder (1986: 9–10) summarized the opinions of conservation biologists working within the zoo community: "Out of a sense of frustration with the limitations of current mammalian taxonomy [broadly using the BSC] in determining which named subspecies actually represent significant adaptive variation, those assembled at the Philadelphia conference [of zoo biologists] willingly discarded the concept that all subspecies are equal. Rather, it emerged that zoos ought properly to address the conservation of evolutionary significant units (ESUs within species)." They went further to suggest that identification of ESUs be made on the basis of concordance across multiple kinds of data and that "when geographic distribution data indicate the existence of *discrete* [italics added] populations within the range of a species, an estimate of genetic distance, for example, should be made to determine whether the populations have ESU status." It is fairly clear what these conservationists were getting at: the traditional BSC approach to individuating units of nature was not working for their purposes. While the determination of whether a population could be judged to have "significant adaptive variation" verges on nonoperationalism, the key recommendation of their proposal—identifying discrete populations—does not. They grasped the reasonable idea of trying to conserve and manage (in situ and ex situ) diagnosable and distinct populations, or ESUs as they were called.

A very large literature has since developed within conservation biology on the concepts of species, ESUs, and other recently introduced terms such as "management units." Systematists have pointed out that ESUs have broad equivalence to the species units identified by the phylogenetic species concept and that use of the PSC meets the needs of the conservation community not currently satisfied by the BSC (Cracraft, 1991, 1997; Vogler & DeSalle, 1994; Barrowclough & Flesness, 1996). Other conservation biologists, notably those having a population genetic approach to the problem, have continued to support the BSC and seek ways to refine theoretical and practical approaches to the ESU concept (e.g., Moritz, 1994a, b, 1995).

There is, however, a powerful and crucial argument often left out of these debates: if conservation biology is to be a science that relies on a rigorous description of diversity, then it should adopt the language and conventions of systematic biology and taxonomic practice (Cracraft, 1997; Wheeler, 1997). Although systematists may argue vehemently over which species concept is best, they agree on many issues of formal taxonomy—that species-level taxa have formal Latin names, that those names are tied to type specimens, that there are standard rules of nomenclature (the international codes) so that scientific names can be organized and managed over time, and that there must be voucher specimens to document taxonomic decisions and descriptions. None of this is found in concepts such as ESUs or management units.

Conservation biology should therefore abandon such concepts as evolutionarily significant units. ESUs are not a substitute for formal taxonomy. Unlike formally described taxa with their types and historical continuity in rules of nomenclature, ESUs cannot have "legal standing." ESUs cannot, and should not, be the units we regulate in trade, protect with legal instruments, or expect to be used by applied biology for biotechnology, biodiversity information systems, and many other uses. This is not the case with *taxonomic units* (Geist, 1992). Thus, the power of systematics and taxonomy: despite arguments over the most fundamental units of nature—species—protagonists share disciplinary standards that prevent names, and thus the identified taxa themselves, from devolving into chaos over long periods of time.

THE SECOND GREAT QUESTION: HOW MANY SPECIES ARE THERE?

Discovering and describing Earth's taxonomic diversity is the starting point for all biological knowledge. Because of its scope and complexity, however, knowing how many species inhabit Earth's ecosystems is one of the megascience questions of biology. While it is generally accepted that around 1.5–1.7 million species have been discovered and described, estimates of unknown diversity range anywhere from 10 to 100 million species, with 13–20 million being the most frequently seen number (e.g., Stork, 1999). So the answer to this megascience question is: We don't know!

But we must find out. When one realizes that the use of biodiversity drives the world economy and this has come from knowledge of about 1.5–1.7 million species—probably less than 10% of all species on planet Earth—it is clear that abundant new benefits will flow from newly documented diversity. Among these benefits of inventories identified by SA2000, one could include:

- they document patterns of diversity across habitats and ecosystems
- they provide baseline data for monitoring activities
- they identify areas of endemism and regions in need of conservation and protection
- they discover new species having economic and social value to societies (pharmacological, agricultural, fisheries, biotechnological)
- they provide the baseline data for implementing an ecosystem approach to conservation and sustainable development
- they support and promote tourism.

We are disastrously ignorant of the natural world. That this is so was highlighted in the 45th Annual Systematics Symposium of the Missouri Botanical Garden (Richardson, 2000), which summarized the need for, and challenges to, systematic inventory (e.g., Prance et al., 2000; Lundberg et al., 2000) and also highlighted that we are in a new age of discovery (Donoghue & Alverson, 2000). We know so little that even in the most well-known groups such as birds and mammals, new species are being discovered each year (e.g., Giao et al., 1998; Beresford & Cracraft, 1999; MacKinnon, 2000). The most outrageous and spectacular example of this is probably the description of six new species of lemurs (in three separate genera) from Madagascar, all published in the year 2000 (250 years post-Linnaeus) in a single issue of the *International Journal of Primatology* (Thalmann & Geissmann, 2000; Groves, 2000; Rasoloarison et al., 2000).

THE THIRD GREAT QUESTION: WHAT IS THE TREE OF LIFE?

Reconstructing the Tree of Life (TOL) is the third great question of systematic biology. This is also a megascience question for systematics for several well-known reasons. First, given N taxa, there are N − 1 nodes that need to be resolved. The consequence is that as the solution to the second great question of systematics—How many species are there?—plays out, the domain of this third question gets larger and larger. A second major reason relates to the first: as the number of taxa in the tree increases, it gets more and more difficult to obtain sufficient data on these taxa, and the computational complexity of finding an objective answer also becomes astronomical. Compared to deciphering the TOL, the determination of the sequence of the human genome, which for all intents and purposes was solved by a single, relatively small corporation, turned out to be a rather simple problem (it just required a little money and coordination among scientists). In contrast, as a scientific problem, resolving the TOL is much more comparable in complexity, say, to knowing all the genes in the human genome, how they function, and how their gene products interact to form a blueprint for development.

So the answer to the third question is, of course: we don't know. As an index to the vastness of the problem, we can estimate that there are right now about 1.7 million nodes on the TOL, reflecting the number of species that have been discovered and described. Yet, where do we stand presently? No one knows for sure, but roughly—very roughly—perhaps 50,000 to 60,000 species are represented on one kind of tree or another. That is a pure guess inasmuch as there is no comprehensive database of trees. The only repository approaching what is needed is TreeBASE [TreeBASE], which has approximately 12,000 taxa, but the sample is highly biased in being mostly botanical.

Assuming 50,000 taxa already placed on one or more trees, it is fair to say the position of most of those is poorly supported by character evidence. While it is perfectly accurate to say our knowledge of the TOL is growing very rapidly, as measured by the numbers of phylogenetic papers being published, it is equally accurate to say a large percentage of the nodes on those trees have relatively little support. There are many reasons for this, among the most important being poor taxon and character sampling, poor choice of character system, and ambiguities in the methods used to analyze the data. Moreover, because taxon sampling is generally poor in most published phylogenetic studies, it is not at all clear how the different results can be linked with one another to form a general view of the TOL, a "supertree of life" if you will.

The most remarkable observation is that our understanding of the TOL—at least in terms of the 50,000 taxa just mentioned—is a product mostly of the last decade. Modern phylogenetics is only about 30–40 years old, and serious "tree thinking" not much older. The rise of "evolutionary systematics" in the 1930s and 1940s, with its emphasis on a population biology/genetic approach toward the history of life, slowed the discovery of the TOL because it was largely assumed that if ancestors could not be found in the fossil record, there was little hope of understanding phylogeny.

If that seems a misrepresentation of history, one only has to examine the content of the major systematics journals (for example, *Systematic Zoology*) prior to 1960 to see that depicting relationships as trees was not of major importance. There was remarkably little "tree thinking" prior to the intro-

duction of numerical taxonomy, a discipline that created trees, but was ambivalent in its interpretation of them. Many proponents of this approach saw their trees as purely representational of phenetic similarity, not history; others hoped these diagrams might reflect some trace of history. The important point here is that, compared to evolutionary systematics, numerical taxonomy developed repeatable methods that produced trees.

Both evolutionary systematics and numerical taxonomy were eclipsed by Willi Hennig's conceptual and methodological development of phylogenetic systematics, or cladistics. The broad adoption of cladistics formalized tree-thinking in terms of phylogenetic relationships and history. Also, the numerical methods that were rapidly introduced brought a much needed objectivity, both philosophical and analytical, to the study of phylogeny. The explosion of phylogenetic knowledge over the last decade has resulted just as much from the conceptual and analytical revolution of the 1960s to 1980s as it has by the introduction of efficient methods to gather new kinds of data, especially those from molecular sequences.

Why phylogenetics matters

These advances in phylogenetic theory and methodology have revolutionized systematic and comparative biology, and the transformation of systematics into a truly historical science could not have come at a better time. Society is desperate for knowledge about phylogeny. While many systematists still see an understanding of phylogeny as a goal in itself, numerous segments of society are looking to phylogenetics to solve entirely new kinds of problems. Consider the following examples:

1. Tracing disease transmission

The first application of phylogenetic analysis to examine disease transmission employed parsimony analysis to investigate whether a Florida dentist, discovered to be HIV-positive and who had contracted AIDS, had transmitted the infection to any of his patients (Ou et al., 1992). These investigators chose the HIV envelope (env) gene because of its high variability and compared sequences from the dentist to those of HIV-positive patients and HIV-positive nonpatients as controls. Phylogenetic analysis showed clear patterns of genetic relationships between the dentist and at least five of his patients who had no identifiable behavioral risks to contract HIV infection (Fig. 1; for discussion of other uses of phylogenetic methods in analyzing HIV evolution, see Holmes et al., 1996, and Crandall, 1999).

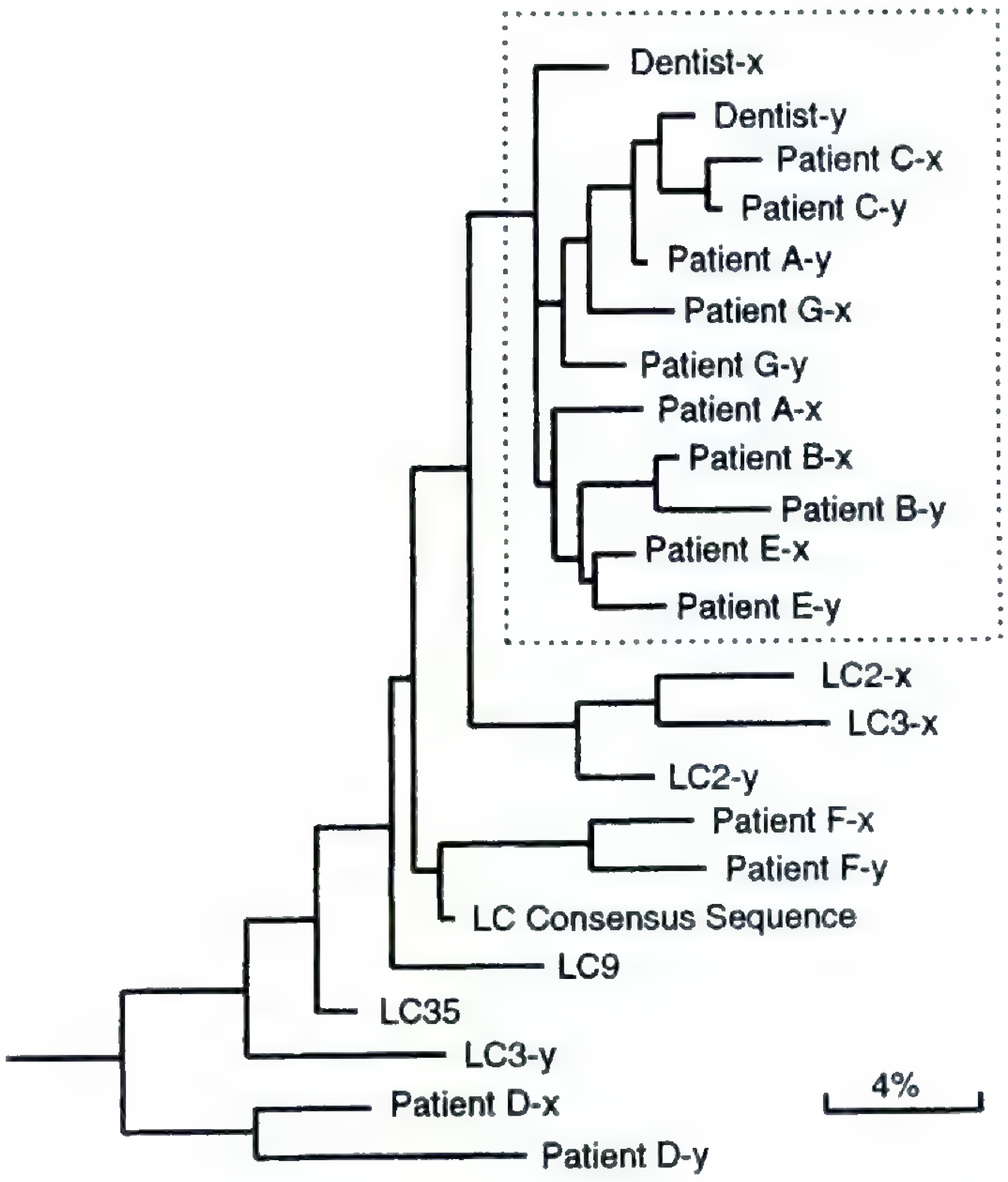

Figure 1. Phylogenetic tree of HIV-1 env V3 sequences from a HIV positive Florida dentist and his patients A–G (x and y notations refer to divergent clones, LC refers to local controls; see Ou et al., 1992, for details). These results were consistent with the hypothesis that the dentist was the source of the patients' HIV infection. This was the first use of phylogenetic analysis to examine disease transmission. Reprinted with permission from Ou et al. (1992), *Science* 256: 1165, figure 1. Copyright 1992 American Association for the Advancement of Science; http://www.sciencemag.org.

2. Tracking the spread of "emergent" diseases

Phylogenetics is playing an increasing role in the medical sciences, especially in identifying disease agents that spread from one region of the globe to another. DNA sequences from disease entities can be rapidly obtained and compared to sequences housed in databases such as [GenBank]. The summer of 1999 in the New York City area brought a strange confluence of events. A number of people were stricken with an encephalitis that had the etiology of a flavivirus. At the same time large birds, including American crows (*Corvus brachyrhynchos*), were turning up dead in unusual numbers in the wild and in local zoos. Viral particles were eventually isolated and their polyprotein nucleotide sequence determined. Phylogenetic comparison with other sequences identified the newly emergent disease as being related to West Nile Virus (Fig. 2; Lanciotti et al., 1999), which circulates between birds and mosquitos and from the latter into humans. Similar strains in the Mediterranean region and Middle East were also associated with increased avian mortality. The virus has now spread

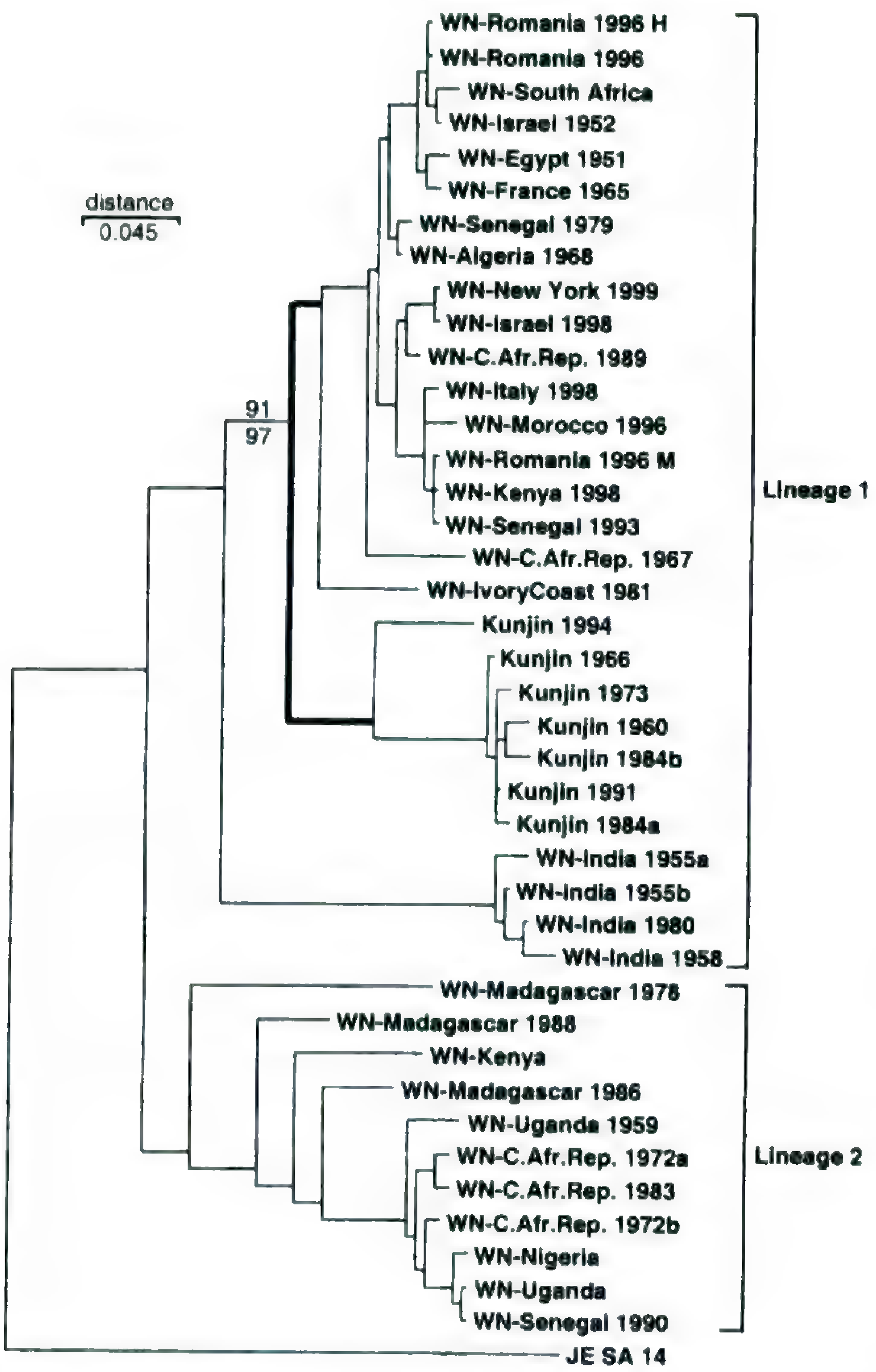

Figure 2. Phylogenetic analysis was used to trace the origin of the West Nile-like virus that broke out in the New York City region in 1999 (Lanciotti et al., 1999). These results indicate the New York strain is closely related to strains from central and northern Africa, the Middle East, and eastern Europe and was derived from that region. Reprinted with permission from Lanciotti et al. (1999), *Science* 286: 2333, figure 2. Copyright 1999 American Association for the Advancement of Science; http://www.sciencemag.org.

well beyond the New York region and also into nonhuman mammalian hosts.

3. Discovery of "new" emergent diseases

In addition to tracking diseases from one region to another, phylogenetic analysis is being used to discover new disease entities. In late 1998 and early 1999 a new mosquito-borne virus, called Nipah, emerged in Malaysia (Chua et al., 2000). Using pigs as a vertebrate host the virus jumped to humans, causing symptoms that first suggested Japanese encephalitis. Eventually 265 cases were reported and 105 people died from severe nervous system pathology. To control the epidemic, over a million pigs had to be slaughtered.

Phylogenetic analysis played a major role in helping to characterize Nipah virus (Chua et al., 2000). Comparative sequences were obtained from the nucleoprotein (N) gene and compared to other members of the subfamily Paramyxovirinae. The resulting tree demonstrated the relationship of Nipah to another recently discovered virus, Hendra virus, and the sequence differences indicated they were distinct (Fig. 3).

4. Monitoring and predicting viral host switching

Karposi's sarcoma virus is endemic to central Africa and has associated with it a rhadinovirus, Karposi's-sarcoma-associated herpesvirus (KSHV). Until recently rhadinoviruses (γ_2-herpesviruses) were found in various Old and New World monkeys but not human's closest relatives, the great apes. After determining sequences of herpesvirus DNA polymerase taken from wild *Pan troglodytes* and *Gorilla gorilla* from Cameroon and Gabon, Lacoste et al. (2000) reported the discovery of new strains of these viruses. When those sequences were compared to others already known using a phylogenetic analysis, Lacoste et al. (2000) showed that these new viruses are closely related to KSHV (Fig. 4). The phylogenetic closeness of these new herpesviruses and KSHV raises the potential for host switching into humans as they hunt and consume great apes for food. Phylogenetic analysis contributes importantly to identifying and monitoring this new health threat.

5. Genomics, development, gene expression, and disease

Phylogenetic thinking and methodologies are taking hold in the fields of genomics and molecular medicine (e.g., Eisen, 1998; Pollock et al., 2000) and promise not only to increase our knowledge of the relationships of organisms but also surely will lead to insights into understanding and predicting gene structure and function. Developmental biologists have long acknowledged the predictive and explanatory power of phylogenetic relationships in reconstructing the historical pathways of development (reviewed in Raff, 1996), and the rapidly expanding field of evolutionary development ("evo-devo") will, reciprocally, result in major new advances in understanding developmental mechanisms and will inject new character systems into systematics that will inform phylogenetic relationships of major organismal groups.

6. Identification of invasive species

The transport of alien species is a major global environmental problem. The United States alone

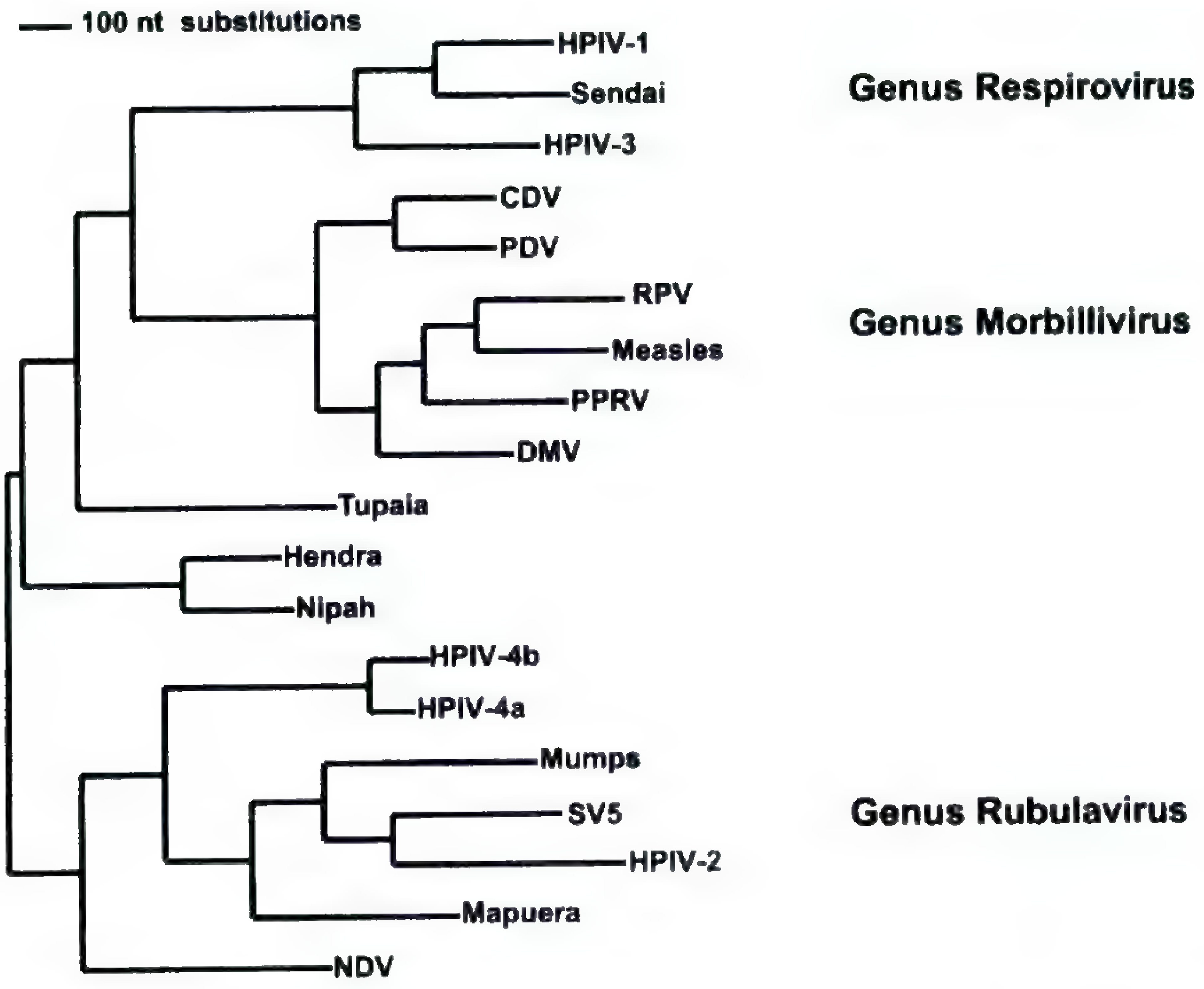

Figure 3. Phylogenetic analysis of the nucleoprotein (N) gene of the so-called Nipah virus that broke out in Malaysia in 1998 and 1999 (Chua et al., 2000) showed this new emergent virus was closely related to another recently discovered paramyxovirus, Hendra virus. Reprinted with permission from Chua et al. (2000). *Science* 288: 1432, figure 4. Copyright 2000 American Association for the Advancement of Science; http://www.sciencemag.org.

harbors about 50,000 invasive species at a loss of nearly $137 billion annually to control and mitigate their effects (Pimentel et al., 2000; Wolfenbarger & Phifer, 2000). Identifying potential exotic species is a major priority and a first-line of defense against them. In 1984 a tropical marine green alga (*Caulerpa taxifolia*) escaped from an aquarium and invaded the Mediterranean Sea. This particular strain proved remarkably hardy and competitive, and spread rapidly to devastate populations of native species (Jousson et al., 2000). The species was recently discovered at several locations along the California coast. Jousson et al. (2000) posed the question whether the California populations of *Caulerpa* could be identified as an invasion of the Mediterranean strain, representing a potentially serious threat to coastal ecosystems. Comparing DNA sequences from the internal transcribed spacer of ribosomal DNA from multiple populations, phylogenetic analysis united 11 of 12 sequences from samples in California with those from the Mediterranean; one sequence clustered with a Red Sea/IndoPacific clade (Fig. 5). It was concluded that an immediate eradication program was warranted.

7. Discovery of microbial diversity

Phylogenetic analysis of DNA sequences has become a major tool in the discovery of new microorganisms, especially bacteria. Because most of these organisms cannot be cultured, microbiologists have turned to molecular probes for inventory and identification (Pace, 1997). Typically using probes for rRNA genes, the sequences are compared to those in databases by various phylogenetic techniques. Phylogenetic methods have thus opened up entirely new approaches to understanding the microbial diversity of extreme environments (Horikoshi & Tsujii, 1999) and have led to a greater understanding of the distribution of microbial life forms. It is now appreciated, for example, that archaebacteria are not only found in extreme environments such as hydrothermal vents and hot springs but are much more widespread than previously thought, including a variety of coastal and open ocean habitats (DeLong, 1992).

THE FOURTH GREAT QUESTION: WHAT HAS BEEN THE HISTORY OF CHARACTER TRANSFORMATION?

The proposition that the history of character transformation might be considered a great question of systematics may strike some as a bit strange, but reflection will confirm that all we know about the evolution of form and function derives from how character change is interpreted relative to a given tree. There have been two main ways in which character transformations are studied. First, in generating phylogenetic hypotheses under maximum parsimony, characters used to build the tree are optimized on it thus allowing inferences about their transformation across the tree. A second method has been to take some tree as given and then optimize, or plot, characters on it. There is a growing

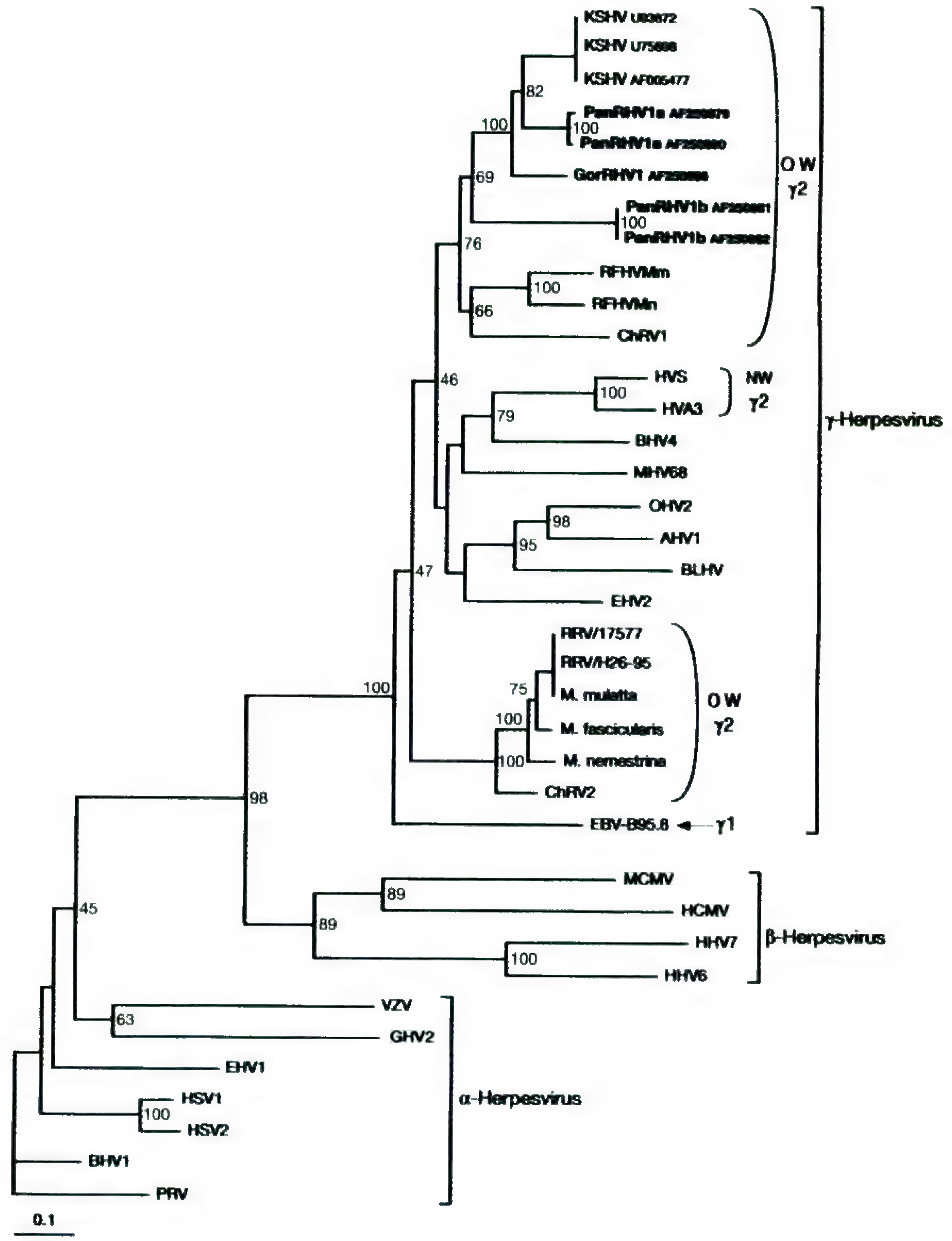

Figure 4. A phylogenetic tree based on sequences of the DNA polymerase gene for several herpesviruses newly discovered in the chimpanzee (*Pan troglodytes*) and lowland gorilla (*Gorilla gorilla*) in Cameroon and Gabon (Lacoste et al., 2000). These results indicated these new viruses were closely related to the Karposi's-sarcoma-associated herpesvirus (KSHV) found in humans. This suggests the possibility that the new herpesviruses might be transmitted to humans since chimps and gorillas are frequently used for food; thus, phylogenetic analysis can be used to predict possible outbreaks as well as help establish a monitoring program for new infection. Tree modified and reprinted with permission from Lacoste et al. (2000), *Nature* 407: 151–152, figure 1. Copyright 2000 Nature; http://www.nature.com/.

literature arguing and demonstrating empirically that the first approach is to be preferred, primarily because the characters of interest are often determinative with respect to choice of most parsimonious tree. The second approach tacitly presumes that the characters being examined have little or no phylogenetically relevant information, which is seldom true.

Nevertheless, the second approach of plotting organismal attributes on a phylogenetic tree will remain popular and exceedingly important. Indeed, the main benefit that nonsystematists gain from a

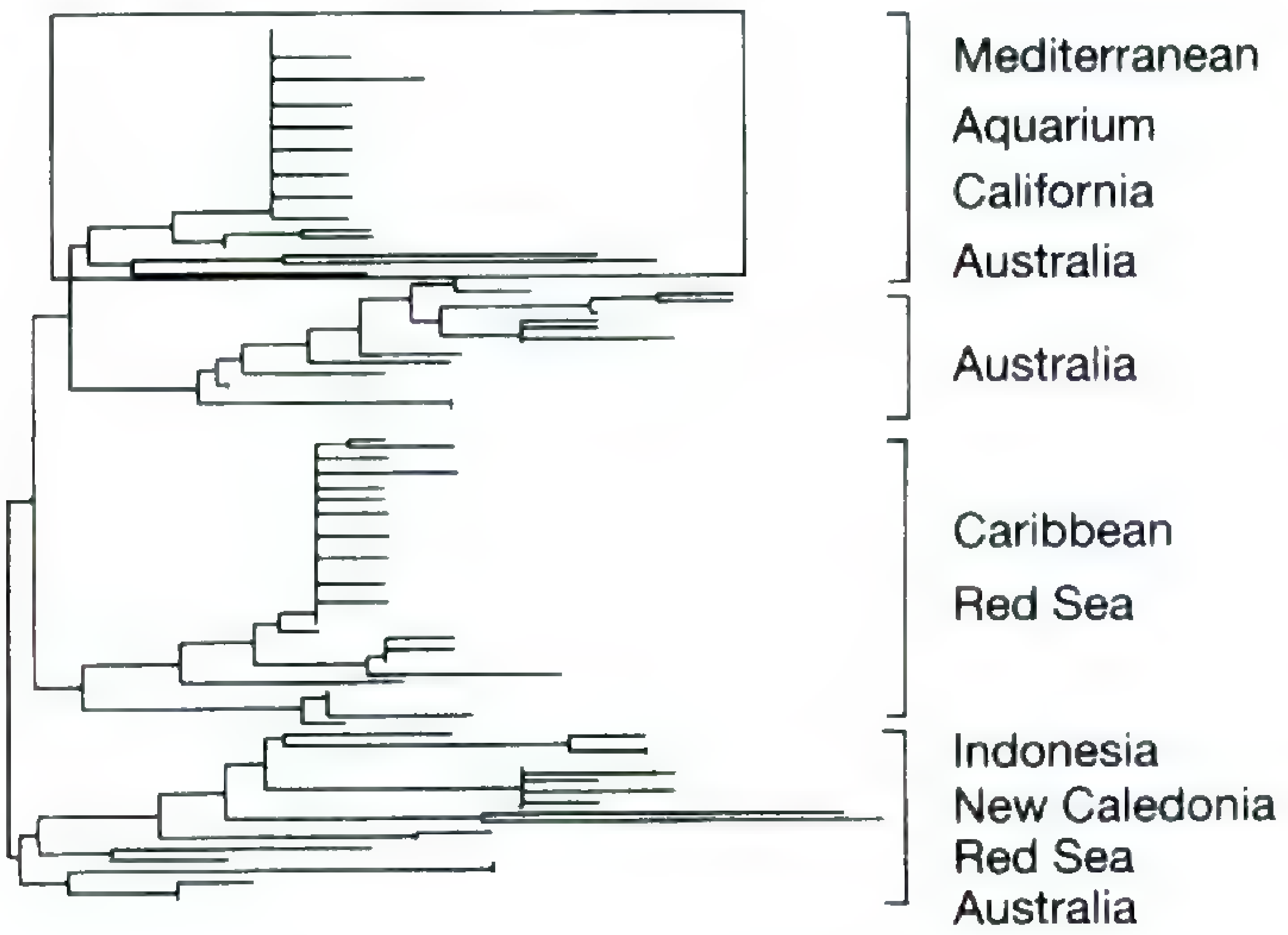

Figure 5. Phylogenetic analysis was used to ascertain the place of origin of a recently discovered invasive alga (*Caulerpa taxifolia*) along the California coast (Jousson et al., 2000). Comparing sequences from the internal transcribed spacer of ribosomal DNA among different algal strains, it was found that the California strain clustered with those from the highly invasive strain that has caused considerable damage in the Mediterranean. This suggested the need for an immediate eradication program. Reprinted with permission from Jousson et al. (2000), *Nature* 408: 157–158, figure 1b. Copyright 2000 Nature; http://www.nature.com/.

fuller understanding of the Tree of Life is that it helps them understand the history of characters and make predictions about taxa for which those characters are yet unknown. Significantly, many of the users of phylogenetic information are themselves contributing data about character systems that will potentially inform our understanding of relationships.

Literally hundreds of papers have used phylogenies to interpret nonsystematic data, and there is no question that this has led to numerous insights into the history of many character systems in behavior, ecology, physiology, and other sciences (e.g., Harvey et al., 1996). More important, perhaps, will be the power of character transformation analysis in applied biology. It has been used, for example, to guide the search for new pharmaceuticals or biochemical products (see Monson, 1996, for review), understand the history of gene regulation (Peterson & Davidson, 2000) and body complexity (Graham et al., 2000; Cameron et al., 2000), among others. Answers to the fourth great question will take on more importance as phylogenetic knowledge and comparative databases expand and become more available.

THE FIFTH GREAT QUESTION: WHERE ARE EARTH'S SPECIES DISTRIBUTED?

This is the most fundamental question of biogeography and any answer will only be as good as the inventories on which it is based. Thus, knowledge of distributions relies on the presence of georeferenced specimens housed in the world's natural history collections. Ultimately, the characterization of Earth's habitats and ecosystems depends on these data, as does the ability to manage and conserve biodiversity.

The practical importance of having knowledge of species' distributions is acknowledged by the desire of nations, intergovernmental organizations, and nongovernmental conservation organizations to have specimens in natural history collections databased and made freely available on the internet. The development and availability of geographical information systems (GIS) and other software programs for mapping diversity are also increasing the value of digitally captured specimen data (e.g., Funk, 1997). Although such data are increasingly coming online, most of the world's collections are not databased. This has led some governments, most notably Mexico, to accelerate data acquisition on their own. The value of their efforts has been well documented (e.g., Bojorquez-Tapia et al., 1994; Soberón et al., 2000) and recognized the world over, as evidenced by the formation of the Global Biodiversity Information Facility [GBIF].

Distributional information for individual species leads to the search for patterns of diversity at different scales. Most importantly, this builds knowledge about areas of endemism, and discovering areas with high numbers of endemic taxa (sometimes referred to as "hotspots") is widely considered critical for setting conservation priorities (Forey et al., 1994; Nielsen & West, 1994; Nielsen, 1999). But distributional data have a much larger significance for society than simply that associated with conservation. Distributional information tied to specimens underlies drug discovery, ecotourism, trade in natural resources, pest control, control of invasive species, crop improvement using the genetic diversity of wild relatives, and analysis of global change, among many other applications.

THE SIXTH GREAT QUESTION: HOW HAVE SPECIES DISTRIBUTIONS CHANGED OVER TIME?

This great question of systematics, and the second pertaining to biogeography, can be looked at in two ways. First, in the here and now: The vast majority of research and activity in "biogeography" is in ecological biogeography, in which ecologists attempt to understand and explain why organisms are distributed where they are, how those distributions are tied to autecologies, and so forth. Yet, without accurate taxonomic descriptions and georeferenced

data vouchered by specimens, the quality of the ecology itself will suffer. A component of this research also looks to the future. Human activities are transforming the biosphere and there is interest in predicting how this impact will affect the distributions of organisms and, downstream, societal well-being, especially for critical activities such as agriculture.

The second way of thinking about changes in distributions is through the eyes of the historical biogeographer. Following the introduction and application of cladistic methods to distributional problems (Rosen, 1978; Nelson & Platnick, 1981), interest in the biogeographic history of taxa and areas of endemism expanded significantly. As was realized early on, the key to understanding the history of biotas is through an analysis of the history of areas of endemism (e.g., Cracraft, 1986). Areas of endemism are evidence that components of biotas (species) have become isolated and differentiated, and nested areas of endemism are evidence that biotas have expanded through dispersion to become more or less cosmopolitan, only to divide again. Yet, reconstructing this history has not been easy. It has become clear that most of these historical patterns of distribution are so complex that no single method of analysis—at least not one that is currently known—is capable of giving a completely satisfying resolution. Each method of biogeographic analysis, it appears, has various shortcomings in how it handles widespread taxa, redundant distributions, and missing taxa and areas, in addition to the fact that the history of areas itself may not always reflect a hierarchical (branching) pattern.

THE SEVENTH GREAT QUESTION: HOW IS PHYLOGENETIC HISTORY PREDICTIVE?

The third mission of systematics, as identified by SA2000, was to create an efficient, and predictive, systematic information system. This included databasing specimens and making the information widely available, linking to other biodiversity and biological databases, and building informatics capacity to utilize biological—and systematics—knowledge globally. The predictive element was envisioned as coming from using phylogenetic classifications to guide searches for information, and thus reflect the hierarchical relationships of life.

The expectation that closely related taxa share similarities not shared with more distant taxa is the foundation for comparative biology. An information system that is queried using the hierarchical relationships of life can be termed *phyloinformatics* (the power of "phyloinformatics" was noted in an NSF-sponsored workshop [Tree of Life] and as well as by Edwards et al. (2000). Thus, the ability to search multiple databases using the nodes of a phylogenetic tree may be the single most important contribution of systematics to conservation and sustainable use of biodiversity. Searches that query across databases of various kinds from the perspective of phylogenetic groupings would therefore have immense predictive power because the resulting data can be expected to reflect attributes shared by, or potentially shared by, those groups.

Discussion: The Future of Systematics and Its Relevance

DIVERSITY

A safe prediction is that debates over the species question will continue. However, I think there is far more actual agreement among practicing systematists than could be concluded by recent papers supporting the BSC. This comment is not to disparage these viewpoints. Rather, it is to reaffirm the opinion of others (Nixon & Wheeler, 1990; Wheeler, 1997) that taxa, and taxic limits, as well as the rules governing names, are the primary domain of practicing systematists. And adjudicating taxic limits, moreover, is very much a practical process: as taxa are analyzed with the purpose of understanding patterns of character variation, geographic distributions and endemism, relationships, and biogeographic history, we will more and more need a species concept that looks at basal taxonomic units. That is the trajectory of research by young systematists doing these kinds of studies, and that trend will certainly continue.

But fighting over species limits is not the frontier of the theme of diversity—rather it is discovering and describing the other 95+% of life. Society needs to know what species share the planet with us, and the urgency has never been greater. Inventorying life's diversity is a megascience question because of its enormous intellectual and technical challenges. Even understanding how to inventory a single taxonomic group in a circumscribed region is a difficult problem (e.g., Coddington et al., 1991), let alone thinking about what approaches and designs of inventories might be appropriate for investigations that are global in scope (Wheeler, 1995a; Wheeler & Cracraft, 1996). A global inventory of life will therefore require meticulous long-term planning and capacity building in infrastructure and human resources, and it will be expensive. But it should be a shared expense of governments, intergovernmental institutions, and the private sector.

Indeed, the private sector is getting involved, and with a larger imagination than currently witnessed within most governmental and intergovernmental circles. Thus, a consortium of technology leaders with a track record in futurist thinking have recognized the need for a global inventory of species and are beginning to organize a long-term effort to see the job accomplished [All Species Inventory]. Because of this brilliant and far-sighted effort, inventory should take on new life!

PHYLOGENETIC HISTORY

In the previous section so much space was devoted to phylogenetics and the Tree of Life because it is often not widely realized, even in the systematic community, how crucially important that branch of systematics is becoming. Phylogenetic knowledge is exploding and the rate at which this is happening will not diminish for quite some time. Problems that undermine the quality of phylogenetic research are commonplace and unfortunately will probably continue to persist. Many non-systematically trained biologists, almost all using molecular data, have paid scant attention to taxonomic documentation, nomenclatural issues, or to proper vouchering of sequences by reference to specimen data. Failure to heed these problems will lead to errors and even to potentially dangerous conclusions in fields like human health (Ruedas et al., 2000). Systematists need to work with editors and editorial boards of journals, and with data depositories like GenBank, to improve this situation.

There is a tacit assumption on the part of many researchers building trees from molecular data that their results are inherently superior to those relying on morphological data. Results are presented, with little or no discussion, and often outright dismissal or total ignorance, of prior morphological studies. This attitude developed soon after molecular studies were introduced (the "molecules versus morphology" debate; e.g., Patterson, 1987), and as I said, it continues.

This conflict is likely to increase as high through-put methods of genomics find their way into laboratories doing comparative phylogenetics. The vast majority of current studies utilize small taxon samples and molecular data samples, leading to a significant accumulation of questionable results because of sampling artifacts. But this situation is changing. As methods improve and more resources are allocated to molecular work, more studies are significantly expanding the sizes of matrices in terms of both taxa and characters. Thus, I predict there will be an increasing tendency to think that molecules alone are yielding the "true" tree of life. But this would be a big mistake. All major groups of living taxa have many long-branched lineages that are monotypic or have relatively few closely related species, and these will in all likelihood continue to confound analysis of deep-branch relationships. To resolve those relationships satisfactorily, it will almost certainly take the addition of morphological characters, especially those from fossil taxa. The relationships of many higher taxa, such as mammals and birds and many others, have been exceedingly difficult to resolve because of the problems just mentioned, and our future hope of understanding the history of life will lie in using all available data.

Applied phylogenetics, as it might be termed, is an easily identifiable wave of the future. One of the most remarkable signs of the vitality of phylogenetics is the expansion of its use into human health, developmental biology, forensics, natural resource management, and other areas. A large number of phylogenetically oriented young systematists are seeking careers in the biotechnology and genomics industries where understanding of phylogenetic methods, and a comparative approach to problem-solving, are needed. This trend will continue for a long time to come.

BIOGEOGRAPHY

Given the current state of knowledge of global biodiversity (5–10% known), and given that most of the species (insects) already described are known from only a handful of localities, it is fair to conclude that we have very imprecise knowledge of the distributions of Earth's species (although single localities could be interpreted as being fairly precise). The task ahead is daunting because virtually all of Earth's habitats and ecosystems have been incompletely inventoried, even for well-known groups such as birds (e.g., Peterson et al., 1998) and mammals (Patterson, 2000). Although an increase in our knowledge about distributions will ultimately be linked to the intensity of inventory efforts, electronically capturing and correlating what we have already collected will surely increase our understanding of distributions and patterns of endemism.

Biodiversity cannot be managed or conserved without distributional information, thus the undeniable importance of databasing the world's natural history collections. Moreover, as global climate change accelerates, and as the anthropogenic conversion of habitats continues, predictions about the

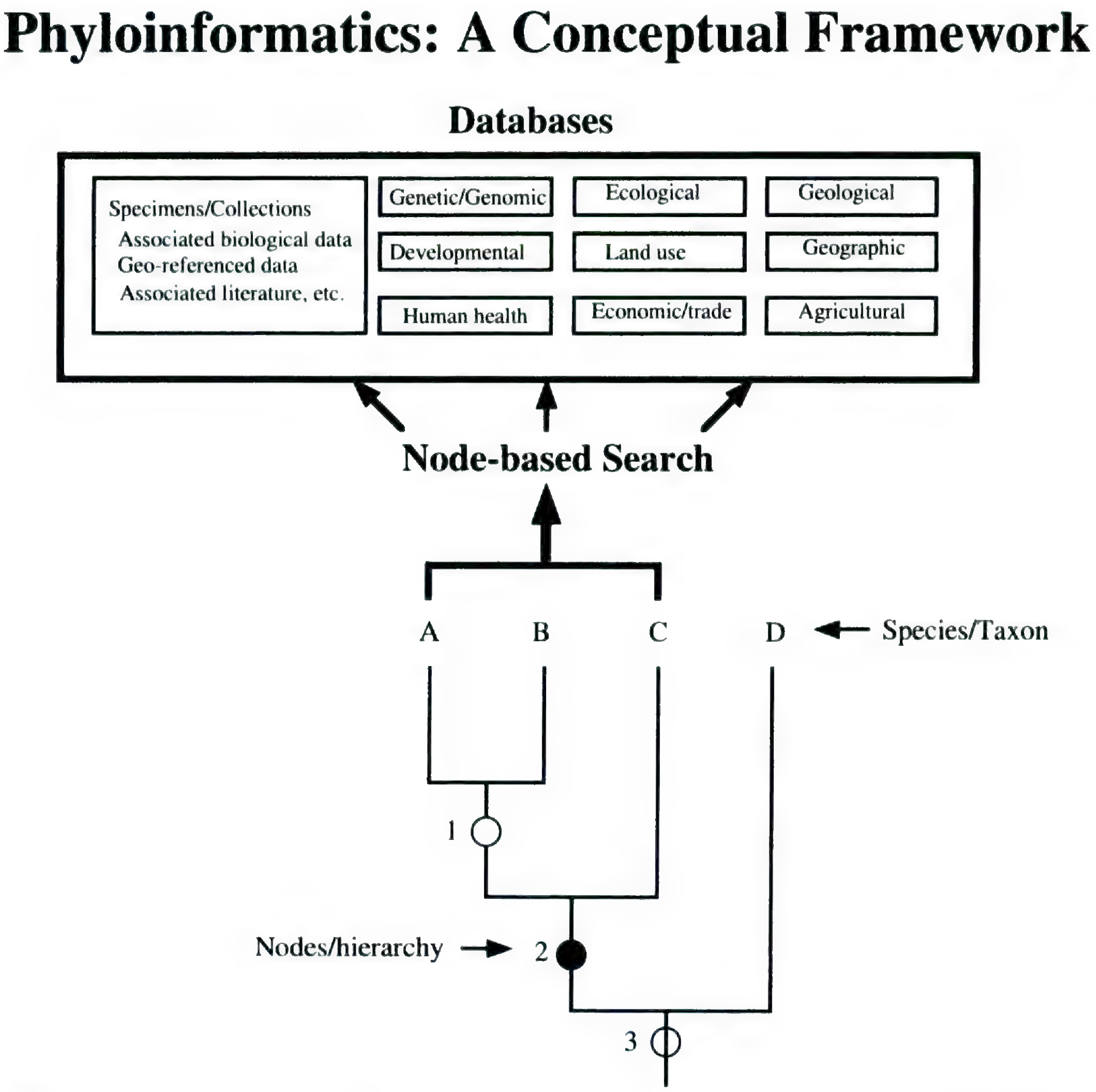

Figure 6. The concept of a phyloinformatic search strategy uses the hierarchy implied by knowledge of phylogenetic relationships to drive queries among multiple databases. Instead of undertaking searches one species at a time, nodes of a tree could be used to power searches for information shared by related species. Here, searches on node (or lineage) 2 would query for information for all species/taxa (A–C) above that node. This figure was first used in a NSF workshop on the [Tree of Life] held at Yale University in July 2000.

consequences of these changes become more and more important. Many of those predictions will flow from the use of historical distributional information linked to specimens.

Biogeography is one of the great frontiers of systematic research. Factors such as widespread, redundant, and missing distributional data hinder understanding of biotic history, but these problems themselves suggest that the field is still wide open to theoretical, methodological, and empirical research. Knowledge of biogeographic history is so central to understanding patterns and processes of biological diversification, including speciation, as well as to how biotas evolve over time, that it will continue to be a core area of research for many years to come. There have been very few studies of biotic history that integrate patterns of relationships among areas of endemism with information from paleontology, paleoclimatology, and paleogeography. There is an unfortunate disjunct, on the one hand, between paleontologists who study diversification over time and rarely concern themselves with present-day patterns and processes such as speciation, and those neontologists who look at patterns of historical biogeography using distributions of the Recent biota but who rarely incorporate paleontological data on changing diversity. A bridge will have to be built before we have a satisfactory picture of biotic history.

PHYLOINFORMATICS

I predict that phylogenetics will have its greatest societal impact by empowering and enriching the search for information and data associations across many different kinds of biological and systematic databases. Information flow will make peoples' lives better. That is what phyloinformatics can, and will, do.

While queries of biodiversity databases will always make use of species' names as pointers to information (Bisby, 2000), the use of node-based queries can expand and integrate searches and information to another order of magnitude (Fig. 6). Phylogenetic classifications will facilitate a new way of gathering biological information and linking it to other nonbiological databases. The establishment of the Global Biodiversity Information Facility ([GBIF]; see Edwards et al., 2000) on 1 March 2001 holds the key to making biodiversity information readily accessible to all. Phyloinformatic queries will expand the potential of GBIF in ways not previously imagined.

The predictive power of phyloinformatics, based as it is on an understanding of the relationships among Earth's species, argues persuasively for discovering all branches of the Tree of Life as rapidly as possible.

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Internet Resources

[All Species Inventory]: http://www.all-species.org/
[DIVERSITAS]: http://www.icsu.org/diversitas/
[GBIF]: http://www.gbif.org/
[GenBank]: http://www.ncbi.nlm.nih.gov/
[GTI] Global Taxonomy Initiative: http://www.biodiv.org/spec-tax/gti/index.html
[TreeBASE]: http://phylogeny.harvard.edu/treebase
[Tree of Life] NSF Workshop Reports: http://research.amnh.org/biodiversity/features/tol.html

TAXONOMY AND HERBARIA IN SERVICE OF PLANT CONSERVATION: LESSONS FROM MADAGASCAR'S ENDEMIC FAMILIES[1]

George E. Schatz[2]

Abstract

Our actions during the next two decades will largely determine how many of the world's ca. 300,000 species of vascular plants will survive for future generations. The fundamental data that define both the taxonomic frameworks within which species are circumscribed and delimited from related species, as well as the geographical distributions of those species, reside in the world's ca. 3000 herbaria. These herbaria, and the taxonomists who work in them, can and must play a critical role in identifying as rapidly as possible those species most threatened with extinction. A project that has focused on the species in Madagascar's seven endemic plant families has demonstrated the necessity of reviewing, and then revising when necessary, the existing taxonomic framework. Comprehensive databasing and georeferencing of primary occurrence data then facilitated simple GIS analyses of Extent of Occurrence, Area of Occupancy, estimates of the number of "subpopulations," and their presence/absence in protected areas, all of which are parameters that contribute to an expedient preliminary assessment of extinction risk. In addition, simultaneous mapping of all species in the endemic families revealed centers of species richness and endemism of particular conservation importance: both those already incorporated in the protected areas system, and, more importantly, those that currently fall outside of the protection network. Partnerships among the world's herbaria can efficiently achieve an initial global assessment of the most threatened vascular plant species by focussing on taxa endemic at political and regional (e.g., Hotspot) scales. The synthesis and analysis of the primary data housed in the world's herbaria—our only incontestable record of plant life on Earth—constitutes the most effective and robust means of directly informing conservation planning, and thereby minimizing the loss of plant diversity.

Key words: conservation, natural history collections, primary occurrence data, taxonomy.

As the term "biodiversity" has entered the international lexicon of the environment during the past decade, one of the most fundamental aspects of the concept has often been neglected: principal knowledge of biological diversity emanates from the study of natural history collections by taxonomists. Plant taxonomists utilize herbarium specimens to erect taxonomic frameworks within which species are defined, circumscribed, and delimited from related species. In addition to portraying the limits of variability of individual taxa, those herbarium specimens representative of a given taxon also constitute primary occurrence data that collectively depict the verifiable (i.e., vouchered) geographical distribution of the taxon. Thus, herbaria, and the taxonomists who examine, classify, and curate the primary specimen data that reside in herbaria, furnish the "what," "where," and "when," initially necessary to document plant life on Earth. As such, they have a unique and critical role to play in global efforts to mitigate the loss of biodiversity. Recent studies of the families of vascular plants endemic to Madagascar (Schatz et al., 2000a) demonstrate that central to such a role is the revisiting, reattributing, and synthesis of the primary data itself.

Tens of thousands of plant species have already been listed as threatened with extinction. The *1997 IUCN Red List of Threatened Plants* (Walter & Gillet, 1998), *The World List of Threatened Trees* (Oldfield et al., 1998), and their to-be-revised-yearly electronic Internet successor, *2000 IUCN Red List of Threatened Species* (see [IUCN]), serve as sober-

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Table 1. Malagasy endemic plant families: Revised (since 1998) taxonomic frameworks.

	No. of species	Newly recognized	Newly described	Placed into synonymy
Asteropeiaceae	8	3 (38%)	2 (25%)	—
Didymelaceae	2	—	—	—
Kaliphoraceae	1	—	—	—
Melanophyllaceae	6	1 (17%)	1 (17%)	4
Physenaceae	2	—	—	—
Sarcolaenaceae	60	25 (42%)	23 (38%)	—
Sphaerosepalaceae	18	2 (11%)	—	—
Total (%)	97	31 (32%)	26 (27%)	4

ing baselines on the state of the Earth's plant resources. As commendable as these efforts are, the fact remains that the majority of plant species have not yet been evaluated with regard to their risk of extinction. As would be expected, the lists are heavily biased in their representation to the comparatively well-known floras of Europe and North America, and to a lesser degree Australia and South Africa, or to specific taxonomic groups (e.g., conifers, palms) or life forms (e.g., succulents) popular in cultivation. One suspects therefore that the number of threatened plant species identified thus far is only the tip of the iceberg. In the absence of an exhaustive survey of all ca. 300,000 (or more?) species of vascular plants (Prance et al., 2000), a strategy to identify and safeguard those remaining species most at risk of extinction must be implemented as rapidly as possible. How can the daily work of herbaria and taxonomists contribute to such a strategy and thereby directly inform conservation planning?

Conservation Assessments Based on Old Taxonomy Will Be Inadequate and Misleading, Because They Fail to Include Recent Primary Data: Revisiting the "What"

The goal of the Endemic Families of Madagascar Project has been to provide current assessments of the conservation status of all species in the seven families of vascular plants endemic to Madagascar and the Comoro Islands (Schatz et al., 2000a). An essential first step in that process was the reevaluation of existing taxonomic frameworks for each of the families, four of which were originally subsumed within non-endemic families: Asteropeiaceae within Theaceae (Perrier de la Bâthie, 1951); Kaliphoraceae and Melanophyllaceae within Cornaceae (Keraudren, 1958); and Physenaceae within Capparaceae or Flacourtiaceae (Perrier de la Bâthie, 1946). The available taxonomy prior to our review dated on average to 1952 (ranging from 1937 to 1963). Reevaluation of existing taxonomic frameworks entailed examination of all primary specimen data. In the case of three of the families—Didymelaceae (Leandri, 1937), Kaliphoraceae, and Physenaceae—together comprising just five species, the most recent frameworks remain valid. But in the remaining four families—Asteropeiaceae, Melanophyllaceae, Sarcolaenaceae (Cavaco, 1952), and Sphaerosepalaceae (Capuron, 1963)—review of all primary data necessitated their taxonomic revision (Randrianasolo & Miller, 1999; Schatz et al., 1998, 1999a, b, 2000b, 2001; Lowry et al., 1999, 2000). In all but one instance, a synoptic format for the revisions was adopted for the sake of expediency: the revised taxonomic framework was illuminated through new identification keys emphasizing diagnostic features, and full synonymy for each taxon was given, but only the newly described species were provided with full descriptions. These revised taxonomic frameworks include 31 newly recognized species (or 34% of the 92 total species now enumerated in those four families), 26 of which were newly described; 4 formerly recognized species and a number of infraspecies were placed into synonymy (Table 1). Primary data that had been collected since publication of the former frameworks accounted for 19 (73%) of the 26 newly described species. In the remaining 12 newly described or recognized species, specimens ascribed to other species in the previous taxonomy were judged to represent clearly discernible, distinct taxa based upon morphological and ecogeographic criteria. Conversely, in the cases of species and infraspecies now placed into synonymy, formerly cited specimens, in conjunction with newly available material, revealed taxa that could no longer be distinguished from earlier described species. Clearly, assessments of conservation status based on the taxonomies that existed prior to our reevaluation would have been highly flawed and misleading, and would have failed entirely to account for

one third of the species now recognized in the seven endemic families.

Conservation is All about Geography, but Most of Plant Diversity is Not Geo-referenced: Reattributing the "Where"

Mapping the primary occurrence data upon which a taxonomic framework stands has long been a preoccupation of taxonomists: most revisions include distribution maps of the taxa. Distribution mapping is usually a tedious task insofar as the majority of primary data collected prior to the latter decades of the 20th century are only imprecisely located in relation to population centers or physiographic features of the landscape, but lack the precise geographical coordinates that can now be assigned so easily in the field with Global Positioning System (GPS) technology. As a consequence, most of plant diversity must be *post facto* geo-referenced in order to capitalize on the current revolution in computer mapping and spatial analysis brought about through Geographical Information Systems (GIS) tools. Geo-referencing of primary data representing the Malagasy endemic families has been greatly facilitated by the compilation of a *Gazetteer to Malagasy Botanical Collecting Localities* [Schatz & Lescot, 2001]. Some historical specimens that lack coordinates may simply be impossible to geo-reference to a scale that has meaning for conservation. In the majority of cases, however, geo-referencing can be achieved to obtain a Minimum Mapping Unit of plus or minus one minute of latitude/longitude, more than sufficient for the coarse area estimates used in conservation assessments. Even in cases of uncertainty involving collections known to originate from within protected areas in Madagascar, but without any greater precision, e.g., the *Réserves Naturelles* or *RN* collection series, mapping to the centroid of the protected area polygon still constitutes a valuable reattribution that can be included in area and subpopulation estimates. Of even greater importance is that collections in the *RN* series document historical presence within the protected areas network.

With new and reconfirmed taxonomic frameworks in place that are based on the totality of available primary data, the next step in assessing the conservation status of each species entails analysis of its geography, including the geography of current land cover and threat. Conservation ultimately depends on sufficient space to maintain a viable population, the size of which will vary considerably from one species to another depending upon life histories and habitat requirements. Although ideally one would want to conduct a long-term Population Viability Analysis (PVA) to determine exactly what constitutes "sufficient space" for each species, area measurements calculated directly with GIS tools based solely on the primary occurrence data can provide a rapid first estimate of a species' vulnerability to threat, and therefore a means of prioritizing concern. Among the assumptions inherent in such an initial evaluation are: (1) that the known collections and localities for a given species are a valid reflection of its abundance and distribution; (2) that widespread and common species will be at lower risk than restricted and rare species; and (3) that species occurring within protected areas will be at lower risk than species that occur only outside of protected areas. The *IUCN Red List Categories* (IUCN, 1994; IUCN/SSC Criteria Review Working Group, 1999) serve as a guideline for incorporating the area measurements of Extent of Occurrence and Area of Occupancy into a hierarchical delineation of extinction risk. For example, among the species in the endemic Malagasy families, newly described *Melanophylla modestei* G. E Schatz, Lowry & A.-E. Wolf (Melanophyllaceae) (Schatz et al., 1998), is classified as Critically Endangered (CR) given an Extent of Occurrence less than 100 km^2, an Area of Occupancy less than 10 km^2, and a single known population (Schatz et al., 2000a). On the other hand, *Asteropeia densiflora* Baker is classified as Vulnerable (VU) due to an Extent of Occurrence less than 20,000 km^2 (Fig. 1), an Area of Occupancy less than 2000 km^2 (Fig. 2), and less than 10 known "subpopulations" (the number of non-contiguous occupied cells or cell clusters within the 10 km × 10 km grid utilized to estimate the Area of Occupancy) (Fig. 2) (Schatz et al., 2000a).

In addition to facilitating rapid area measurements that can be incorporated into evaluations of extinction risk, reattributing primary data with geographical coordinates also allows the modeling of potential distribution (Skov, 2000; see also [BIODI] and [Species Analyst]). Utilizing the spatial analytical functions of GIS, an envelope of independent physical and environmental variables associated with a set of primary occurrence data points can be described, and in so doing define an environmental niche, and hence, a potential distribution that corresponds to the range of documented heterogeneity. When compared against current land cover as revealed from satellite imagery, remaining viable habitat coinciding with (preferably recently) documented distribution can be identified. In the absence of extant viable habitat that intersects the documented distribution, i.e., when all historical

Figure 1. Extent of Occurrence (= 17,830 km^2) of *Asteropeia densiflora* Baker in Madagascar.

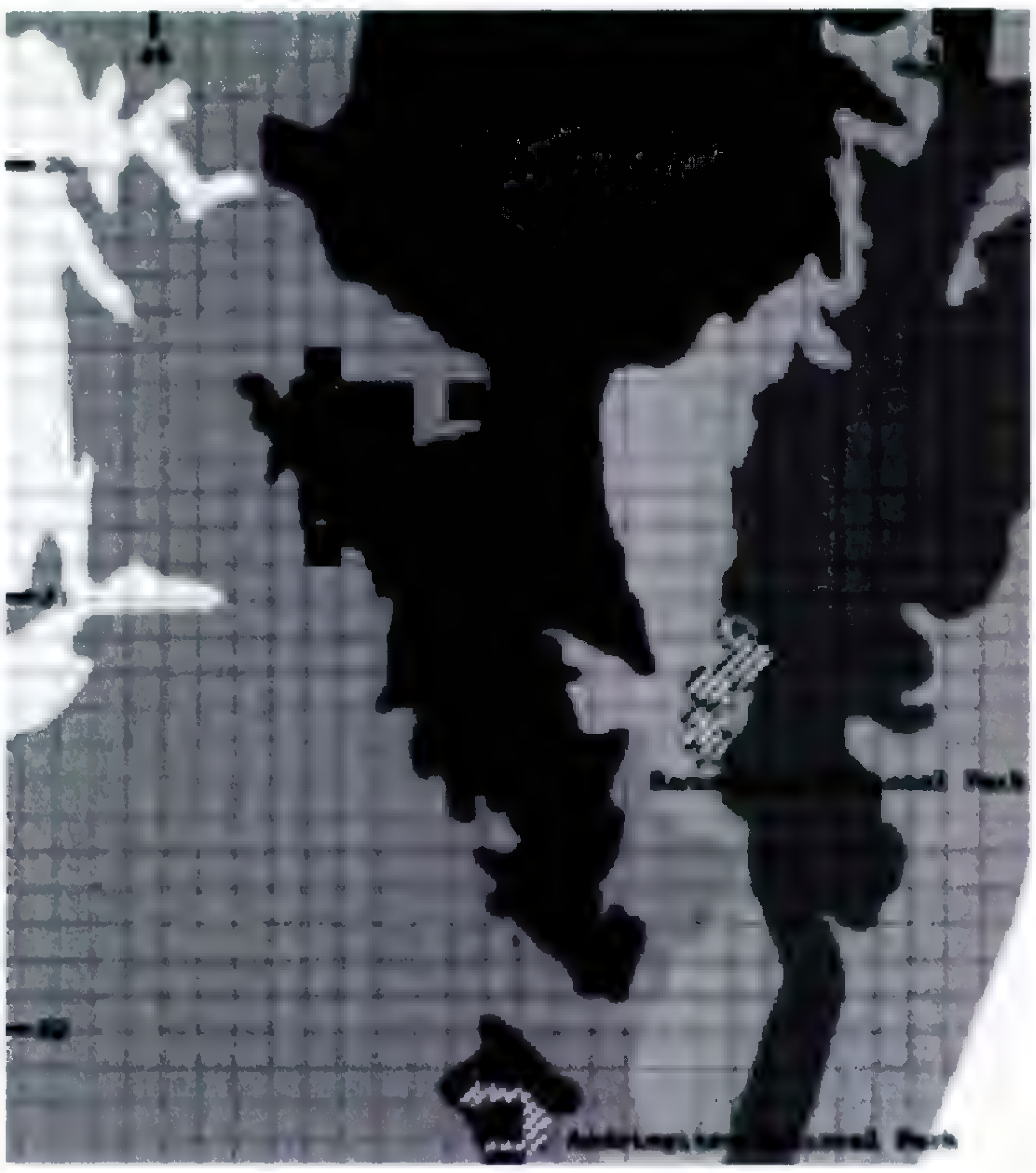

Figure 2. Area of Occupancy (= 1800 km^2) and number of "subpopulations" (7 individual cells + 2 cell clusters = 9) of *Asteropeia densiflora* Baker in Madagascar as defined by a 10 km × 10 km grid.

primary data originate from areas now converted to urban or agricultural uses, conservation hopes for a species may still lie within areas of potential distribution and remaining viable habitat.

Conservation in such places as Madagascar may ultimately depend upon encompassing a species within some type of protected area. An overlay of protected areas polygons in relation to primary occurrence data instantly reveals if a "gap" in protection exists. Among the 97 species in the seven families endemic to Madagascar, at least 28 species are not presently recorded from protected areas. The situation is potentially far bleaker for the species endemic to Ecuador, where over 75% of the 4011 endemic species are not yet documented in protected areas (Valencia et al., 2000). Similarly, the 1995 revised ROTAP (*Rare or Threatened Australian Plants*) listing (Briggs & Leigh, 1996) reveals that 47% of the 5031 listed taxa are not documented from protected areas. If one goal of conservation is to ensure that the maximum number of species is included within the protected areas network, then considerations of complementarity dictate that centers of endemism, i.e., concentrations of co-occurring local endemic species, be identified (Williams, 1999). For Madagascar, simultaneous mapping of all species in the endemic families revealed, for example, that the Ibity/Itremo Massifs on the Central High Plateau, which are geologically characterized by a complex mosaic of granitic, marble, and quartzite substrates, constitute an important center of endemism that is *not* currently encompassed within the protected areas network. Of the ten endemic families' species recorded from Ibity/Itremo, five (all Sarcolaenaceae)—*Leptolaena diospyroidea* (Baill.) Cavaco, *Pentachlaena latifolia* H. Perrier, *Perrierodendron quartzitorum* J.-F. Leroy, Lowry, Haevermans, Labat & G. E. Schatz, *Schizolaena microphylla* H. Perrier, and an undescribed species of *Xerochlamys/Sarcolaena*—are essentially restricted to the Massifs, and are therefore entirely lacking protection. The presence of numerous other local endemics in the Ibity/Itremo Massifs, including a number of legumes (Du Puy & Moat, 1998), forcefully argues for the immediate establishment of new protected areas in the region. Simultaneous mapping of all species in the endemic families also revealed the importance and management needs of existing protected areas. In particular, the small Réserve Naturelle Integrale of Betampona (2228 ha) shelters 20 species in the endemic families, including two newly described as a result of revised taxonomies within Sarcolaenaceae (*Pentachlaena betamponensis* Lowry, Haevermans, Labat & G. E. Schatz and *Rhodolaena leroyana* G. E. Schatz, Lowry & A.-E. Wolf) that are known only from this reserve. Map-

ping reattributed primary occurrence data of restricted range species, i.e., country endemics, or species endemic to Ecoregions (Olson & Dinnerstein, 2002 [this volume]) or Hotspots (Myers et al., 2000), may well constitute the most efficient and robust means of directly informing conservation planning.

MUCH OF PLANT DIVERSITY IS "RARE," I.E., DOCUMENTED BY VERY FEW COLLECTIONS, AND HERBARIA AND THEIR ASSOCIATED DATA ARE IDIOSYNCRATIC: STRATEGIES AND NEW STRUCTURES FOR RAPIDLY ACHIEVING THE SYNTHESIS OF REATTRIBUTED PRIMARY DATA

Faced with the very real prospect of losing a significant proportion of the estimated 300,000 or more species of vascular plants during the coming decades, it is incumbent upon the systematics community to synthesize the most relevant primary data, and disseminate that data to governments and the conservation community. By definition, such a synthesis must go beyond Red Lists per se as they are currently envisioned by IUCN (see [IUCN]). Although Red Lists attempt to draw attention to the species most at risk of extinction, because they lack the underlying geo-referenced primary data, they have only very limited utility for conservation planning. Nevertheless, Red Lists in their current form, along with country and regional checklists, can help guide the prioritization of primary data synthesis. By identifying the greater than 25% of Ecuadoran species known only from the type collection, and the greater than 50% known from only one or two populations, and conversely, the less than 10% that are "common" (known from ten or more populations), the *Ecuador Red List of Endemic Plants* (Valencia et al., 2000) serves to prioritize which species should be subject to comprehensive primary data synthesis. Similarly, ROTAP lists nearly 200 Australian species known only from the type collection (Briggs & Leigh, 1996). Surely, a comprehensive synthesis of all vascular plant species known only from their type collection, and the geo-referencing of as many as possible, must be one of the very first priorities.

Species known only from a single (type) collection are merely an extreme case of endemism. Within the context of the Convention on Biological Diversity (see [CBD]), governments are obligated to pay particular attention to all those species endemic within their borders. Among the nearly 34,000 species listed in the *1997 IUCN Red List of Threatened Plants* (Walter & Gillet, 1998), 91% were single-country endemics. The recent *Red Book of Iran* (Jalili & Jamzad, 1999) evaluates all 1727 endemic species (22% of the total flora), and the Ecuador *Red Book* focuses solely on the endemic species. What is required next is the assimilation and geo-referencing of the primary data of all of these, as well as every other country's endemic taxa. Priority should be accorded to species representative of endemic higher taxa, i.e., families and genera. A similar approach should be adopted within the framework of the new Critical Ecosystem Partnership Fund initiative (see [CEPF]), which seeks to address conservation needs at a regional scale, as delimited by conservation Hotspots, which are themselves defined in part by a minimum number (1500) of endemic plant species (Myers et al., 2000). Knowing where the endemic species occur (or at least occurred at some point in the past, and might possibly still occur) within countries or regions is fundamental for the rational allocation of finite conservation resources.

But as the review of all primary data representing the Malagasy endemic families has demonstrated, knowing where the endemic species occur must be predicated on knowing just what the endemic species are. Catalogues such as those for Ecuador (Jørgensen & León-Yánez, 1999) and Peru (Brako & Zarucchi, 1993) involve some review of the primary data, but generally do not exhaustively inventory all existing specimens. Revised taxonomic frameworks, however, should in theory be based upon examination of all existing collections, and therefore represent the most appropriate and opportune point at which to disseminate reattributed primary data. Indeed, deposition of reattributed primary data into an Internet-accessible database should be a sine qua non for publication of a revised taxonomic framework, just as deposition of nucleotide sequence data into GenBank (see [NCBI]) has become (in most cases) a necessary precondition for publishing phylogenetic frameworks. For revised taxonomies of the Malagasy endemic families, comprehensive, reattributed (i.e., geo-referenced) primary data have been deposited in the world's largest botanical specimen database, to which Internet access is provided through W³TROPICOS (see [MBG]). Recent discussion of the state of bioinformatics for biodiversity has sounded the call for improved infrastructure, and highlighted various developments involving remote query and retrieval from multiple, so-called distributed databases (= "interoperability") (Bisby, 2000; Edwards et al., 2000; Krishtalka & Humphrey, 2000). Nevertheless, in conjunction specifically with the publication of revised taxonomic frameworks, it would seem appropriate and extremely

Table 2. Representativeness of TROPICOS specimen database on 10 October 2000.

- 1.5 + million specimen records
- 922,668 geo-referenced
- 1.14 million identified to spp. representing 117,806 spp.
- 45,752 spp. (39%) represented by only 1 specimen
- 62,709 spp. (53%) represented by 1 or 2 specimens
- 96,456 spp. (82%) represented by 10 or less specimens
- 4,742 spp. (4%) represented by 50 or more specimens

useful to establish a GenBank analog ("SpecimenBank") for deposition of the underlying geo-referenced primary data. The utility of recent *Species Plantarum—Flora of the World* (see [ABRS]) treatments of Irvingiaceae (Harris, 1999), Stangeriaceae (Steyn et al., 1999), and Welwitschiaceae (Steyn & Smith, 1999) would be significantly enhanced if the underlying primary data were accessible from an Internet specimen database. Just as the nucleotide sequences in GenBank document the microgeography of biodiversity, natural history collections define its macrogeography. Obvious linkages between the two scales should be made, as well as to seedbanks and living germplasm collections (at [IPGRI] and [NPGS]).

Although the TROPICOS database of the Missouri Botanical Garden does contain some exhaustive sets of primary data such as those assimilated in the course of the review and revision of the Malagasy endemic families, in general, it reflects the idiosyncratic, incomplete nature of herbaria and their associated specimen data. The sources of the representativeness of TROPICOS (mostly contemporary collections from a limited number of regions), wherein 117,806 species are represented by 1.5+ million specimens, dictate that the majority of species are represented by only one or two specimens; conversely, only 4% are represented by 50 or more specimens (Table 2). Just as taxonomic revisions require the pooling of primary data from numerous herbaria, the synthesis of such data for conservation must also involve "North/South" herbarium databasing partnerships. For any given country or region of the world, usually a limited number of internal and external herbaria hold the majority of unique primary data. Adopting a species by species approach, and beginning with those endemic to countries and regions, North/South herbarium partnerships should work to synthesize primary data into a global plant conservation database. A model already exists to emulate for the development of such a database. Botanical Garden Conservation International (see [BGCI]) serves as a coordinating body to galvanize ex situ plant conservation efforts at over 500 member botanical gardens, maintaining a database of the ca. 85,000 species currently in cultivation in those gardens. Similarly, the 3000 herbaria worldwide (Holmgren et al., 1990), and indeed, the ca. 215,000+ plant species *not* yet in cultivation, would benefit tremendously from an analogous coordinating body ("Herbarium Conservation International") to help facilitate databasing partnerships for the synthesis of primary data that could directly inform in situ plant conservation. Such a coordinating body would assist in the organization of regional herbarium networks such as the highly successful Southern African Botanical Diversity Network (see [SABONET]), and ensure that they are partnered with the appropriate Northern herbaria. The ongoing Red List Program within SABONET (Golding, 1999a, 1999b, 2000) would be greatly enhanced from formalized partnerships with the Northern herbaria where the majority of primary data from the region are housed.

The task of synthesizing primary data of the most threatened plant species is large, but by no means insurmountable. The analysis of over 4000 Ecuadoran endemic species was achieved within a little over a year of the publication of the Ecuador *Catalogue*. With ca. 300,000 species to track, and 3000 herbaria, each herbarium would need to take responsibility for only 100 species on average. *Index Herbariorum* lists 8800 staff working at the 3000 herbaria; throw in an additional 1200 students and volunteers, and each person would be responsible for collating the primary data of just 30 species on average. In fact, the task is not even that great. There are numerous widespread species of little or no conservation concern (except when their invasive capacity leads to the displacement of indigenous species). The problem should thus be attacked from both ends, identifying both the most widespread and "weedy" species, as well as those represented only by one or several collections. Momentum is building to synthesize information on invasive species globally (see [GISP] and [NBII]), but there is as yet no organized effort to tackle the latter, i.e., the rarest of species. Similarly, great progress (sometimes even with redundant and overlapping efforts) is being made to diffuse the "names" of biodiversity (see [ABI], [IPNI], [IOPI], [ITIS], [Species 2000]). However, as governments and conservation organizations seek to prioritize and protect remaining tracts of viable habitat, it is imperative that they have access to more than just the "what" of threatened biodiversity. "Names" have meaning only in relation to the primary data that

define them: originally by their types, and then subsequently all the other specimens assigned to them by taxonomists in the course of trying to order the grand diversity of life. Therefore, by definition, the meanings of plant "names" cannot remain static. Each new collection expands the meaning in space and/or time, and has the potential to significantly modify or alter the meaning, or even to define a new name. To maximize the number of plant species that will survive the current extinction wave, we must also furnish the "where" of rare and threatened plant species, continually revisiting and reattributing the primary specimen data, our only incontestable record of life on Earth.

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CHICAGO WILDERNESS: A NEW FORCE IN URBAN CONSERVATION[1]

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Abstract

In 1996, a coalition of diverse and determined organizations launched a new initiative in the Chicago region. Our vision? Chicago Wilderness: a thriving mosaic of natural areas, connected by greenways and wildlife corridors, embedded in the nation's third largest metropolis. In this vision, the region's human communities reclaim a cultural tradition of protecting and restoring these globally significant natural communities that enrich our lives. Today, more than 100 organizations join forces to transform this vision into reality. A regional Biodiversity Recovery Plan—the result of three years of assessment and planning by scientists, land managers, educators, and policy strategists—sets priorities and determines the lines of action for the coalition. This regional agenda stems from our vision and recovery goals for each ecological community; it encourages targeted research initiatives that focus on characterizing our native biological diversity and on analyzing elements critical to its recovery. Ultimately, though, the long-term survival of our natural wealth rests on the support from the public. While the challenges to conservation educators and communicators are many, Chicago Wilderness allows us to work together in understanding our audiences, channeling our resources, and creating novel approaches to engage the widest public in our conservation efforts.

Key words: Biodiversity Recovery Plan, Chicago Wilderness, citizen science, coalition, conservation education, forest preserves, fragmentation, metropolis, mosaic, natural communities, oak savannas, oak woodlands, prairies, public outreach, remnants, restoration, urban.

Chicago Wilderness: the Natural Capital

Chicago, the third largest metropolis in the United States, is anything but "untrammeled by man, where man is a visitor who does not remain" in the words of the Wilderness Act (Section 2.c; [Wilderness Act]), which has shaped our modern concept of wilderness. Nonetheless, "Chicago Wilderness" is the emerging force in our urban landscape. Launched in 1996 by a coalition of 34 diverse and determined organizations, Chicago Wilderness joins forces to conserve the globally important natural communities that survive in our metropolis.

The surprise to many is that the boundaries of Chicago Wilderness capture a spectacular array of rare ecosystems: tallgrass prairies, oak woodlands, oak savannas, sedge meadows, marshes, bogs, fens, and other prairie wetlands. In fact, within Chicago Wilderness—which extends in a crescent around Lake Michigan from southeastern Wisconsin, through six Illinois counties, into northwestern Indiana—survive some of the best remnants of the prairie and oak-savanna communities of the Midwest (Table 1). These remnants shelter a number of species that are rare worldwide and that are listed as threatened or endangered in the states of Illinois, Indiana, and Wisconsin. These species once lived in the thriving, expansive grasslands and woodlands that have now been turned into monocultures of corn or soybean.

At the turn of the century, Chicago was blessed with far-sighted planners who created a system of forest preserves in and around the city. In 1900, architects Jens Jensen and Dwight H. Perkins led the Municipal Science Club in Chicago, which worked hard for many years to ensure that the best remaining natural lands were set aside for the public (see Sullivan, 1997; Chicago Region Biodiversity Council, 1999: 19–21). Famous architect and planner Daniel Burnham and fellow architect Edward Bennet also contributed extensively to the cause. The wilderness in Chicago now survives in parcels that range in size from half-acre remnants to the 19,000-acre Midewin National Tallgrass Prairie. Some of the natural remnants survive in old settler cemeteries or along railway rights-of-way.

[1] We thank the members of Chicago Wilderness and of its teams, along with the citizen scientists in the region. Collectively, they are the power behind this regional effort and the focus of this paper.

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Table 1. Remaining natural areas in Illinois (prairies, oak savannas, oak woodlands, prairie wetlands) with high floristic quality.

Region	Original acreage	% Surviving
Galena	371,000	0.00005
Chicago	1,998,000	0.04
West Central	3,217,000	0.00006
Springfield	2,041,000	0.003

Source: The Illinois Natural Area Inventory, Illinois Department of Conservation, 1976.

Most survive in the preserves that total over 200,000 acres (81,000 ha) of federal, state, county, and municipal protected lands and waters. All parcels exist within the much larger matrix of public and private, built and natural lands that support the region's 8 million residents.

Our natural communities suffer from a number of stresses, including habitat fragmentation, interruption of natural fire regimes, air and water pollution, and native and exotic invasive species. The long-term survival of these endangered plant and animal assemblages depends on the proper ecological management and aggressive restoration of degraded lands, even—or primarily—in the region's forest preserves and conservation districts. It is this need for coordinated and rapid action that now brings together more than 130 institutions including landowners, government agencies at local, state, and federal levels, education and research institutions, and conservation organizations to turn the vision of Chicago Wilderness into reality.

Chicago Wilderness: What, Where, and Why

Chicago Wilderness is both the name of the coalition of organizations committed to protecting, restoring, and managing the natural communities in the Chicago region, and the natural communities themselves, along with the plants and animals that depend on them for survival. Chicago Wilderness also is the people of the region, the human residents whose quality of life depends on a thriving regional nature reserve.

Urban living often results in an almost complete detachment of people from the land. An important goal of Chicago Wilderness is to reconnect a landless urban population with the pulse of nature. The name Chicago Wilderness is meant in part to emphasize the connections between wilderness in the conventional sense—in remote and inaccessible places—and wilderness in the places where people live and work.

But why strive for a regionwide coalition instead of working through more manageable, individual collaborations? The answer lies in the realities of the region: extreme fragmentation of the natural communities. The high-quality native patches in the region are tiny. Nothing short of a massive, regionwide, coordinated effort will ensure the long-term survival of these natural communities, through the management of much larger lands that surround and connect the remnants. In the vision of Chicago Wilderness, we reconnect the 200,000 acres of fragmented natural areas through greenways and wildlife corridors. And in this vision, the human communities reclaim a cultural tradition of restoring, protecting, and managing our natural communities.

Chicago Wilderness: the Organization

Chicago Wilderness is a loosely structured organization, with an unconventional organizational chart (Fig. 1). In Chicago Wilderness we are bound by our common goals and objectives and by our collaborative projects. We are in essence a volunteer-driven effort. Four teams focus on the central lines of action: science, land management, policy and strategy, and education and communication. The teams attract participation of many non-member institutions, which adds to the scope and strength of the coalition. Current and past chairs of these four teams and staff from other member organizations form the nucleus of a coordinating group that develops central strategies, maintains momentum, and resolves day-to-day problems. A steering committee of executives in the Chicago Region Biodiversity Council oversees the initiatives, including approval of budgets and projects. The Council encompasses the chief executives of all member institutions: federal, state, and local government agencies; land-owning agencies; research and education institutions; and conservation organizations. These executive, or voting, members elect the steering committee. A proposals committee solicits and reviews proposals for priority conservation projects and recommends funding; the committee has one or two representatives from each of the four teams. And the Recovery Plan Task Force spearheaded the gigantic effort of developing, compiling, and writing the first draft of the Biodiversity Recovery Plan for the region (see below).

A few ingredients have been instrumental in allowing Chicago Wilderness to succeed as a massive coalition. We briefly highlight these below.

(1) A critical mass of people thoroughly—passionately—committed to seeing the work succeed, and ready to put an inordinate

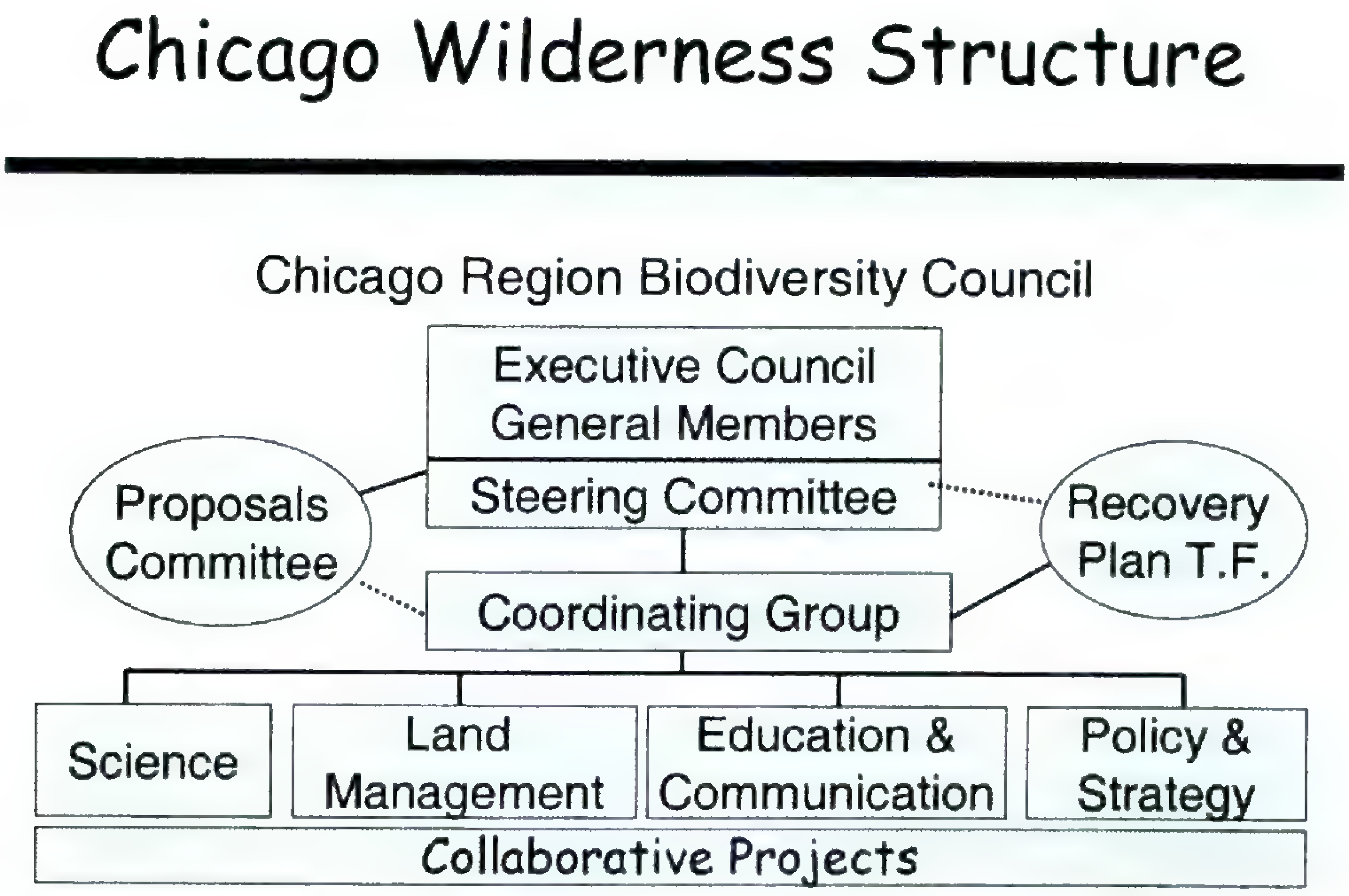

Figure 1. Organizational chart for Chicago Wilderness.

amount of time and effort into making it happen. For us, this core energy came from the coordinating group, with its 12–15 members.

(2) Early, visible, and popular successes. In Chicago Wilderness, these early successes came from some of our public awareness materials. The *Atlas of Biodiversity* (Sullivan, 1997) was the first publication of the Chicago Region Biodiversity Council. It characterizes the natural communities in the region, with their rich assemblages of plants and animals, and helps bring these natural areas to the attention of a very broad audience, most of whom are unaware of the existence of such biological riches in our own backyard. The *Atlas* was one of the first concrete examples of how Chicago Wilderness could help individual members become more successful and effective in their work. The whole region needed a powerful, visual publication about our natural treasures. The *Atlas* is now in its fourth edition, with more than 40,000 copies already distributed; see [Chicago Wilderness publ.].

(3) Mission-related benefits to individual members. For the coalition to thrive, individual members must become more successful in their individual endeavors because of their association with the coalition. Conversely, each member must contribute in its own way and with its unique strengths to the coalition and to the pursuit of the collective mission. For example, one of the goals of The Field Museum is to direct its resources—scientific expertise, worldwide collections, innovative education programs—to the immediate needs of conservation at the regional and international levels and to create a link between academic institutions and the groups most closely tied to biological stewardship. Chicago Wilderness offers the Museum a tremendous advantage in tapping into a wide, regional effort. In turn, with Chicago Wilderness, the Museum has directed much more of its efforts in research, inventory, and tools for conservation to the Chicago region.

The potential for Chicago Wilderness to serve as a model for urban conservation attracted early attention of several federal agencies, including the U.S.D.A. Forest Service, the U.S. Fish and Wildlife Service, and the U.S. Environmental Protection Agency, who have provided significant operating grants since 1996, bringing new conservation revenues to the region. Matching services from members, and funds attracted by members for projects catalyzed by Chicago Wilderness, exceed 70% of the funds dedicated to this regional effort.

Chicago Wilderness: Impact on Scientific Research

Research focusing on local biodiversity and land management issues in the Chicago region has been ongoing for over 100 years. But a recent resurgence of interest in local issues by the region's scientific community was coincidental with, and in large part a consequence of, the founding of Chicago Wilderness. This outcome can be attributed to several reasons, including that the consortium has been successful in bringing new resources to the area to support research. More important than the new funds, however, is that the partnerships and oppor-

tunities for collaboration fostered by Chicago Wilderness have created new research initiatives, identified important research questions, expanded interest in the resulting data, and created an enhanced atmosphere for the importance of biodiversity and ecological research focused on the region.

Several Federal and Illinois State agencies have provided grants to Chicago Wilderness to help enable the initiative to meet its goals. Chicago Wilderness makes requests for proposals each year to distribute these funds to outstanding projects. A proposal committee (see above) reviews submitted proposals and ranks them based first on merit—scientific, educational, policy—and then on the relevance to the mission of Chicago Wilderness and on the degree to which the results will make unique contributions to the initiative; i.e., will serve as a model for other projects or will provide data that may serve as the underpinning for a series of other studies. The topics of funded research proposals fall into one of the following broad categories: Research/Inventory/Monitoring; Restoration; and Tools for Research—imaging projects, database projects, or other conservation tools.

The following exemplars of science projects funded through Chicago Wilderness provide an indication of the breadth of the research undertaken by Chicago Wilderness member institutions. All projects funded through Chicago Wilderness are summarized in www.chicagowilderness.org. Although Chicago Wilderness funds only a small portion of the flourishing biodiversity research activity in the area, it has been greatly responsible for invigorating the interests of scientists in conducting research in the region.

RESEARCH/INVENTORY/MONITORING PROJECTS

Projects within this category focus on increasing our understanding of the native biological diversity in Chicago Wilderness. Research projects concentrate on factors influencing that diversity and on the efficacy of current management practices to maintain and restore the region's native diversity. Funded projects have ranged from studying the effects of restoration efforts in oak woodland communities on a broad group of taxa (fungi, beetles, millipedes, amphibians, mosses, birds, and flowering plants), to documenting the diversity and distribution of the region's bats, to landscape-level inventories of watersheds, to studying the role of arbuscular mycorrhizal fungi in prairie restoration.

RESTORATION PROJECTS

The focus of projects in this category has been (1) to develop best practices transferable to other sites or (2) to restore specific sites of special significance. Funded projects have ranged from developing and testing methods for restoring specific threatened and endangered plants, to restoring a degraded tallgrass prairie at Indiana Dunes National Lakeshore.

TOOLS

The goals of these projects are to develop useful tools that facilitate research and land management activities in the region. These tools include imaging projects to develop multispectral vegetation maps using aerial flyovers, creating an online metadata catalogue of existing spatial datasets owned by Chicago Wilderness member institutions, and using spectral data to track changes in land use and land cover over the region. Funded database projects include compiling data from past breeding bird surveys into a user-friendly database [Bird census] and the development of a database of the current status and location of the region's threatened and endangered plant species [Chicago Wilderness grant]. An example of another type of tool is the development of a user-friendly computer model to analyze strategies for deer removal in different land-management programs [Ecology Software Server].

The continued growth and development of the Chicago Wilderness coalition and the impact that the coalition is having throughout the area, has enhanced communication among scientific researchers, land managers, educators, and policy makers in the region. Such communication is critical for effective development of research programs that enhance the conservation of biodiversity. Through understanding the types of data most needed by the users of research results (i.e., land managers, conservation biologists, policy makers, educators), and how to present these data to the users, we have identified new research projects while enhancing the value of our research and expanding the audience for our results. In turn, the region has gained better recognition of the value of research and has increased opportunities for its continued funding. The positive cycle continues to foster further research activities in Chicago Wilderness.

Our Road Map: The Regional Biodiversity Recovery Plan

From the earliest days of the Chicago Wilderness coalition, member organizations recognized that to be effective, we needed a strong regional conservation agenda with clear priorities for action. The concept was to produce a biodiversity recovery plan, in some ways analogous to a single species

recovery plan, which would provide an assessment of the current conditions along with a road map for how to reach desired vision and goals. An effective recovery plan would help shape decisions at both the policy and the land-management levels.

We completed the plan in late 1999, after almost three years of dedicated work by more than 200 members and nonmembers—including the science, land management, education, and policy experts in the region [Chicago Wilderness biodiversity]. The Recovery Plan identifies the ecological communities of the greater Chicago region, assesses the overall condition of these communities and the threats facing each, lays out the vision and recovery goals for each species assemblage, and recommends actions to achieve our goals. The plan also introduces a process of conservation and information design that leads to coordinated research, inventory, and monitoring agendas to support these conservation goals and strategies and to anchor them on the best available science. And the plan calls for a massive communication effort to galvanize public support behind our conservation agenda.

ANATOMY OF THE RECOVERY PLAN

The plan provides both an overarching vision for what Chicago Wilderness—the land and biodiversity—can become and a broad treatment of the details of how to get there. In developing the plan, we used a consensus-based approach, relying on the region's experts and the available data. The plan also provides the platform for organizing action at a further level of detail, and it provides a strong foundation for communication about the challenges facing biodiversity conservation in the region.

The recovery plan document itself is intended for reference. It is a comprehensive treatment of the central issues, with 11 chapters and 11 appendices (Chicago Region Biodiversity Council, 1999). Chapters cover a summary of the biodiversity values in the region; a history of the changes in the landscape and of conservation efforts to date; key ecological processes that shape and sustain the region's natural communities; the status, needs, and goals of terrestrial and aquatic communities; the status of threatened species; research and monitoring needs; tools for conservation; goals for communication and education; and the role for key players in executing the plan. To present the findings of the plan to broader audiences, Chicago Wilderness developed a smaller, summary document focusing on the important issues and recommendations.

The recovery plan process brought together experts from many backgrounds and disciplines to share their knowledge. The outcome is not only the region's state-of-the-art insights, but also a blending of our science, policy, and communications expertise. The process resulted in heightened interest and commitment for collaboration in more detailed plans for conservation action within a regional context.

The plan contains 140 separate recommended actions that fall into the following six categories:

(1) *Land management.* Most natural areas in the region are not being managed in a manner that will sustain plant and animal diversity over time: more acres need to be under ecological management, and the intensity of management must increase.
(2) *Land protection.* Additional land will need protection as the region's human population continues to grow. The primary concern in setting aside more land for conservation is to create larger, unfragmented protected areas, either de novo or by enlarging existing ones. Since much of the land in natural conditions is either protected already or is in extremely small parcels, the recovery plan envisions the need for restoring to ecological health disturbed and converted areas, such as agricultural lands, as a strategy for creating larger units.
(3) *Stream protection.* We must protect remaining high-quality streams, where most of the remaining aquatic biodiversity resides, from additional degradation.
(4) *Research and monitoring.* Research needs relate primarily to understanding how best to address the threats to biodiversity posed by human development. For monitoring, the plan puts forward a system of adaptive management based on conservation planning (briefly discussed below).
(5) *Education and communication.* The plan recognizes that public understanding and support is a precondition to the success of a long-term, broad-based public undertaking such as biodiversity conservation. The plan lays out steps to achieve increased understanding of the importance of biodiversity and what it takes to conserve it on both short- and long-term scales (see further discussion, below).
(6) *Local and regional development policies.* The region is at a critical time for developing policies that will control anticipated growth in

Table 2. Vegetation communities in Chicago Wilderness: a consensus list developed in 1999 by members of Chicago Wilderness Science and Land Management Teams and by staff of the regional Forest Preserve Districts.

Community classes (8)	Communities (24)	Subcategories (55)
Forested communities	Upland forest	Dry mesic, Mesic, Wet mesic
	Floodplain forest	Wet mesic, Wet
	Flatwoods	Northern, Sand
	Woodland	Dry mesic, Mesic, Wet mesic
Savanna communities	Fine-textured-soil savanna	Dry mesic, Mesic, Wet mesic
	Sand savanna	Dry, Dry mesic
Shrubland communities	Fine-textured-soil shrubland	Dry mesic, Wet mesic
	Sand shrubland	Dry mesic, Wet mesic
Prairies	Fine-textured-soil prairie	Dry, Mesic, Wet
	Sand prairie	Dry, Mesic, Wet
	Gravel prairie	Dry, Mesic
	Dolomite prairie	Dry, Mesic, Wet
Wetland communities	Marsh	Basin, Streamside
	Bog	Graminoid, Low shrub, Forested
	Fen	Calcareous floating mat, Graminoid, Forested
	Sedge meadow	
	Panne	
	Seeps and springs	Neutral, Calcareous, Acid
Cliff communities	Cliff	Eroding bluff, Dolomite cliff
Lakeshore communities	Lakeshore	Beach, Foredune, High dune
Cultural (human-dominated) vegetation communities	Cropland	
	Unassociated growth	Grass, Forb, Shrub, Tree
	Tree plantation	
	Developed land	

population and in urban space in the coming decades. The recovery plan stresses the impact of the region's management of growth on biodiversity and suggests steps to mitigate that impact.

THE PROCESS OF CREATING THE RECOVERY PLAN

The primary units of conservation in Chicago Wilderness are plant communities. Initial natural area inventories for the region, upon which most conservation strategies to date have been based, focused on remnant high-quality communities (White, 1978). The recovery plan also adopts plant communities as its primary conservation targets, but it considers animal communities or assemblages, aquatic communities, and threatened species as well. A critical first step in the plan became to develop and adopt a plant community classification system that all Chicago Wilderness members could accept and upon which the region would base subsequent conservation and land management decisions (Table 2).

Most land management agencies in the region traditionally have classified their holdings according to the community classification system used by the Illinois Natural Areas Inventory (INAI) in the 1970s (White, 1978). Rather than adopt a completely new system for the recovery plan, Chicago Wilderness elected to develop a modified version of the INAI system. The modifications reflect a deeper current understanding of community gradients in fire-dependent forested lands in the region (see Bowles & McBride, 1996). In addition, the new classification places more focus on degraded lands, recognizing those lands as the primary target of restoration efforts. While the Chicago Wilderness classification system does not follow the emerging national standard for community classification (Grossman et al., 1998), the recovery plan includes a crosswalk to these national standards. The resultant community classification system includes 8 major community groups, 24 community types, and 55 subtypes distinguished primarily by soil moisture (Table 2).

While the plan lays out actions covering all of the biodiversity of the region, not only what is unique or rare, it also incorporates a method to identify what is most important from a global perspective and what conservation targets need the most immediate attention. We undertook this evaluation primarily at the natural community level, but also included information from key groups of animal assemblages and of threatened species.

Regional experts first evaluated the status of animal groups or subsets of groups: reptiles and amphibians, breeding birds, mammals, and some terrestrial invertebrates. In workshops, the scientists grouped the species found in the region into broad assemblages associated with habitat types; for example, savanna birds or forest and woodland reptiles and amphibians. These assemblages are not mutually exclusive in that some species will fall into more than one grouping. The experts then assessed the significance of the Chicago Wilderness region to the global survival of each assemblage and its constituent species. The three ranks we used were: Globally Critical, meaning that the Chicago Wilderness region is very important to the overall survival and well-being of the assemblage; Globally Important, meaning that the region contributes significantly to the overall well-being of the assemblage; and Locally Important, meaning that the assemblage is an important component of the region's biodiversity, but its status in the region will not have a substantial impact on the global well-being of the assemblage. Experts also assessed the condition of the assemblage in the region, ranking them as "of concern/declining" or "stable." Combining the rank in importance on the one hand, and the condition of the assemblage on the other, helped to identify the Chicago Wilderness habitats that need most immediate attention to stem declines or to improve conditions. The exercise also helped us to determine the habitats in the region that are most significant in terms of global conservation. The moist grassland bird assemblage came out as both, Globally Critical and in poor condition. Ten other assemblages in Chicago Wilderness are Globally Important and are declining. All of these assemblages and conservation targets are listed in the Biodiversity Recovery Plan.

Prior to evaluating communities, planners also reviewed the threatened plant species in the region and placed them into six categories of priorities, from species that are globally rare to species that may be adequately protected or stable, but are restricted to communities that are rare within Chicago Wilderness. Presence of threatened plant species was an element in evaluating priorities for conservation targets within biological communities.

To evaluate the relative need of different biological communities for additional conservation action, Chicago Wilderness members built on existing methods for ranking endangered ecosystems (Noss et al., 1995; Noss & Peters, 1995). We modified these systems slightly, to include the key factor of condition (quality), which is one of the most significant elements in the sustainability of biodiversity in this urban region. As with the animal assemblages, expert groups convened for one-day workshops over a period of several months to assess available data and to rank natural community types against defined criteria. Four rankings—quantity, quality, biological importance, and contribution to global conservation—combined to make the final ranking. The ranking variables at focus were:

- For quantity—(i) total amount (acres) remaining of the community, (ii) amount lost since pre-settlement, and (iii) number of patches large enough to sustain a relatively intact assemblage of constituent species over time.
- For quality—(i) remaining percent in good quality, (ii) degree of fragmentation and isolation, and (iii) extent and effectiveness of current management efforts.
- For biological importance—(i) levels of species richness, (ii) numbers of threatened species, and (iii) key ecological processes.
- For contribution to global conservation—ranking of communities as (i) endemic to the region, (ii) at the center of the range, or (iii) at the edge of the range. This assessment also considered the effectiveness of conservation efforts for the community type in other regions.

We combined the individual rankings to develop a tiered set of conservation targets, recognizing that all community types will require some degree of conservation effort to survive in the urban landscape. Table 3 shows the first two tiers of community targets. In all, Chicago Wilderness convened 13 daylong workshops (in 1997–1999) for experts

Table 3. Conservation targets for recovery based on status, importance, and distribution.

First (highest) tier
Woodland (all moisture classes)
Fine-textured-soil savanna (all moisture classes)
Mesic sand savanna
Sand prairie (all moisture gradients in dune and swale topography)
Dolomite prairie (all)
Panne
Graminoid fen
Fine-textured-soil prairie (all moisture classes)
Second tier
Dry sand savanna
Gravel prairie (all)
Basin marsh
Calcareous floating mat
Calcareous seep
Sand prairie (other than those in dune and swale topography)
Northern flatwood
Streamside marsh

to rank community types, and to discuss threats and conservation needs. Through a similar process, we evaluated the conservation needs of rivers, streams, and natural lakes in the region.

The ranking system to produce the conservation targets was not quantitative, but it represents a consensus of the experts in the region. Key effort in the planning process went toward developing and adopting a process for further refining our conservation goals, developing strategies to obtain those goals, and setting up monitoring systems that enable information to feed back into refining management strategies toward these goals.

The Chicago Wilderness region adopted a process of conservation design, where planners (1) develop a vision and goals for each conservation target, (2) identify key threats to achieving the vision/goals, (3) set conservation strategies to abate the threats, (4) establish indicators for progress toward achieving the goals, and (5) develop a feedback mechanism to adjust management strategies if monitoring shows progress is insufficient. Chicago Wilderness members are using additional consensus-based expert workshops to develop this iterative process for conservation targets at individual sites and across the entire region. Linking conservation design to efforts that involve citizens in collection of scientific data will help combine the scientific aspects of the recovery plan with education, outreach, and public involvement programs.

Once assembled, the draft of the recovery plan went through a formal, legal hearing process under the auspices of the Northeastern Illinois Planning Commission and the Northwestern Indiana Regional Planning Commission. Both Commissions and several municipal agencies adopted the plan within months of its publication. The value of the formal process was not only to gain feedback from a larger public, but also to seize on the opportunity to raise the issue of biodiversity in fora traditionally concerned primarily or exclusively with development and transportation issues. The final recovery plan is now on a level with other major plans that will guide the development of the region in the years to come. As a result, the issue of biodiversity will be discussed with business and civic leaders along with economic competitiveness, quality of life, and education.

Our Education Goals

Chicago Wilderness realizes that the future of our native landscapes depends on the support and involvement of our citizenry. On the encouraging side, Gallup surveys (1999) and research by Belden and Russonello (1996) reported that most Americans consider environmental protection to be a priority. Concern about air and water pollution is widespread; citizens worry about destruction of tropical rain forests, toxic waste contamination, and habitat loss. But while concern about these issues is wide, it is not deep. Environmental issues often fade when economic matters compete. And biodiversity recovery faces additional challenges: public surveys report that only 20% of the population recognizes the term "biological diversity" (The Biodiversity Project, 1999).

Faced with these challenges, the Education and Communication Team of Chicago Wilderness has adopted (1) short-term communication strategies coupled with active public involvement projects, while (2) building and implementing longer-term educational strategies. To guide our actions, the more than 200 educators in Chicago Wilderness have embraced the internationally held definition of Environmental Education:

> "Environmental Education is a learning process that increases people's **knowledge** and **awareness** about the environment and associated challenges, develops the necessary **skills** and expertise to address these challenges, and fosters **attitudes,** motivations, and commitments to make informed decisions and take **responsible action**" (UNESCO 1978: 15; highlights added).

The boldfaced words (our emphasis) spell out the five components essential for making a program in biodiversity education result in changed behavior and in informed decision-making. Chicago Wilderness Educators have used these five components—awareness, knowledge, attitudes, skills, and participation—to develop a matrix that assesses our existing programs, from birth to death, against our targeted objectives.

Table 4 presents an abbreviated sample of this education matrix. An "X" indicates presence of the component in that program. For example, the BETA project incorporates all five essential components. Our compilation revealed that while our programs are strong in awareness and knowledge, they are weak or altogether lacking in attitude clarification, skill development, and active participation. To address these gaps and to reach the 80% who have never heard of biological diversity, while also ensuring that our education systems produce biologically literate graduates, we adopted program guidelines that (1) extend the scope of our existing, successful programs to include attitude, skills, and action components; (2) develop new programs that specifically address the lacking components; (3) reach beyond our current circles by working with community-based organizations; (4) expand the dis-

Table 4. Sample matrix of existing programs in conservation education. An "X" indicates presence of the component in that program.

Target audiences	Existing resources	Essential components of biodiversity education				
		Awareness	Knowledge	Attitude	Skills	Participation
Children (Pre-School–8th & Teens)	An Atlas of Biodiversity	X	X			
	Chicago Tribune Biodiversity Supplement	X	X	X	X	
	Biodiversity Education Through Action (BETA) Project	X	X	X	X	X
	Chicago Wilderness Communication Tools	X	X			
	Mighty Acorns Expansion Program	X	X	X	X	X
	IDNR Biodiversity of Illinois CD-ROM Series	X	X	X	X	
	EcoWatch	X	X	X	X	X
Adults	An Atlas of Biodiversity	X	X			
	Chicago Wilderness Magazine	X	X			
	Chicago Wilderness Communication Tools	X	X			
	EcoWatch	X	X	X	X	X
	It's Wild in Chicago	X	X	X		

tribution of our successful educational tools; and (5) ensure that students in the Chicago Wilderness region—from elementary through university—are literate in biodiversity.

Promoting programs jointly, creating complementary (rather than competitive) projects, sharing teacher-education expertise, and submitting collaboratively developed proposals to schools are some of the new ways in which Chicago Wilderness reaches adults, children, and educators for greater impact. For example, Mighty Acorns is a stewardship program for eight- to ten-year-olds created by The Nature Conservancy. This highly successful program used to be limited to a few schools in one county. Today, through the leadership of Chicago Wilderness and two of its members (The Nature Conservancy and The Field Museum), the program has expanded to 19 Chicago Wilderness organizations in six counties in Illinois and one in Indiana, and it involves 90 schools, 210 teachers, and 6500 students. The majority of these 6500 students come from underserved communities. These elementary students are engaged actively in learning about the region's plants and animals, experiencing nature, and practicing ecological stewardship—removing buckthorn and garlic mustard, collecting and planting seeds—to improve the health of our natural communities in the Chicago region.

Chicago Wilderness also has partnered with large distribution networks, like the Chicago Tribune's Newspapers in the Classroom program, to develop and promote a curriculum and activity guide on the biodiversity of the region, using the Chicago Wilderness Atlas as the central teaching tool. Through its website and a printed brochure, Chicago Wilderness provides to all in the region a full list of the local educational resources and how to obtain them [Chicago Wilderness publ.].

Public Involvement and Outreach

To inform the public about pressing issues related to the protection of our natural communities and to engage a large constituency in the support and work of restoration, the Biodiversity Recovery Plan outlines the following priorities:

- Increase the public's understanding of the role of ecological management
- Foster grassroots involvement in restoration and conservation activities
- Expand opportunities for "citizen science"
- Engage a wide public as volunteers

One opportunity that fosters wide public involvement is an annual spring event, "It's Wild in Chicago." The four-day festival attracts thousands of visitors to interact with Chicago Wilderness members at their displays through featured performances, hands-on activities, and targeted programs. The festival provides a forum for the public to learn about Chicago's wilderness and for Chicago Wilderness to reach new audiences with our messages.

Our National Public Lands Day event, another effort fostered by Chicago Wilderness, enhances family involvement as volunteers and the engagement of a wide public in exploring the role of ecological management in the survival of our native communities. In 2000, more than 6000 people participated in restoration activities at 21 Chicago Wilderness sites.

Through a program of the Illinois Department of Natural Resources (IDNR; [EcoWatch]), hundreds of citizens—adults and high-school students—gather data on the ecological condition of rivers, forests, wetlands, and prairies in Chicago Wilderness. Several more hundred "citizen scientists" gather targeted data on birds and butterflies in the region. In many instances, the volunteers themselves enter the data on-line, to be analyzed by regional scientists and land managers, and by the state. Through our process of conservation design, we are now tying the data collection by citizens to the needs of land managers in monitoring and revising their management efforts.

As a result of Chicago Wilderness, Field Museum scientists and educators partnered with IDNR to develop [UrbanWatch] with the following goals:

- Record the presence and distribution of groups of organisms—plants, animals, fungi—in an urban environment (we selected organisms that can be used to assess the condition of natural areas in urban centers)
- Examine environmental factors that influence the biodiversity in urban ecosystems
- Analyze and compile the information in a way that is readily usable by urban planners and park managers.

Focused on city parks, cemeteries, golf courses, corporate campuses, schoolyards, backyards, and tree-lined streets, UrbanWatch collects data to examine environmental factors that influence the native diversity in urban green space. Urban planners, park districts, site managers, and landowners will have access to these data and will apply them in the management of sites to improve or create urban spaces that are friendly to native communities and that address the needs of migrating birds and butterflies in our region.

Our Communication Opportunities

Significant current challenges in ecological restoration require immediate strategies to increase public awareness and understanding. Chicago Wilderness has complemented its long-term approaches in public involvement, with actions aimed at achieving the following short-term goals for communicating about biodiversity to the general public:

- Recognize biodiversity in everyday experiences
- Understand human impacts on biodiversity
- Recognize the connection between healthy nature and quality of life

The Chicago Wilderness Communications Team has adopted the successful approach to crafting messages developed by the Biodiversity Project (1999) in Madison, Wisconsin. The approach advocates having a clear goal and target audience, identifying core values of the target audience that the message embraces, and writing the message in short paragraphs. These paragraphs address (i) why the issue is important to the audience (leading with values), (ii) what the threats are and who is responsible, and (iii) what people can do to address the threats. Through this method, the message directly incorporates the values of the audience. Equally important, each message ends with an action that the target audience can easily undertake.

We developed a number of attractive and highly effective communication tools using this method, including a video, tabletop display, and slide show [Chicago Wilderness]. These tools are available to all Chicago Wilderness members, to deliver a consistent, compelling message. Protecting Nature in Your Community, a companion piece to the Biodiversity Recovery Plan, is one of our tools that focuses on reaching public officials, policy makers, municipalities, zoning boards, and the over 300 governing bodies that review and guide the design of hundreds of proposals for land development and redevelopment every week. For the general public, the *Chicago Wilderness Magazine*, currently with over 9000 subscribers, is sold at local bookstores, including Barnes & Noble and Borders, at gift shops of our member institutions, and at other outlets.

While the challenges to conservation education and communication are many, the Chicago Wilderness coalition enables us to work together in understanding our audiences, challenging our resources, and creating novel approaches to engage the widest public in maintaining and restoring our local biodiversity.

Chicago Wilderness began with a larger-than-life goal: nothing less than rescuing vibrant natural areas by transforming the environmental culture of the people responsible for them. Through the partnerships formed and the collaborative work, Chicago Wilderness is proving itself equal to the task. From scientifically rigorous approaches in ecologi-

cal inventory, restoration, and monitoring to creative advances in planning, policy, education, and outreach, the accomplishments of Chicago Wilderness are building a living legacy for the future.

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SAFEGUARDING SPECIES, LANGUAGES, AND CULTURES IN THE TIME OF DIVERSITY LOSS: FROM THE COLORADO PLATEAU TO GLOBAL HOTSPOTS[1]

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Abstract

Hotspots of biodiversity have become priority areas for land conservation initiatives, oftentimes without recognition that these areas are hotspots of cultural diversity as well. Using the Colorado Plateau ecoregion as a case study, this inquiry (1) outlines the broad geographic patterns of biological diversity and ethnolinguistic diversity within this ecoregion; (2) discusses why these two kinds of diversity are often influenced by the same geographic and historic factors; and (3) suggests what can be done to integrate traditional ecological knowledge of indigenous peoples into multicultural conservation collaborations.

Key words: biodiversity, conservation planning, linguistic diversity, traditional ecological knowledge.

"Along come the scientists and make the words of our ancestors into folklore."

—Agnon (1966)

"The diversity of life on earth is under threat; so is the diversity of human cultures. . . . The intriguing question is this: apart from establishing rights over resources, will the local communities bring back some of their earlier cultural traditions of conservation of biological diversity?"

—Gadgil (1987)

The Colorado Plateau of North America (Fig. 1)[3] has received international recognition for nearly a century because of the pioneering efforts there to formally protect its spectacular natural and cultural landscapes (Sellars, 1997). Despite that recognition, the region's resource managers and conservationists have yet to work with much understanding of how biological and cultural diversity have interacted within this four-state area. Since the establishment of Mesa Verde National Park in 1906 and the Grand Canyon National Park in 1919 (Burnham, 2000), more than 11.1 million acres of the Colorado Plateau's 130 million acres have been federally protected for their natural and cultural resources. A diverse collection of national parks and monuments, wildlife refuges, recreation areas, conservation areas, preserves, wilderness areas, and national historic parks and sites, these protected lands are managed by the National Park Service, the U.S. Fish and Wildlife Service, the U.S. Forest Service, and the Bureau of Land Management (Tables 1 and 2). Conservation efforts on the Colorado Plateau were initiated long before our belated recognition that the ecoregion harbors a remarkably high diversity of plants, butterflies, tiger beetles, and mammals compared to 109 other ecoregions of similar size in North America (Ricketts et al.,

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[3] As far as we are concerned, an "objective" definition of the Colorado Plateau does not exist. Different researchers draw the Plateau's boundaries differently, but most agree that the Plateau's geographic heart is located in the Four Corners region, where the states of Arizona, Utah, Colorado, and New Mexico intersect. The three figures included in this essay show two different boundaries of the Colorado Plateau, especially along the northeastern margin. For the purposes of statistical analysis (of the total area of Indian lands versus federally protected lands, etc.) in this study, we used the Colorado Plateau boundary outlined in Figure 3. The boundary shown in both Figures 1 and 2 is an "alternative" delineation.

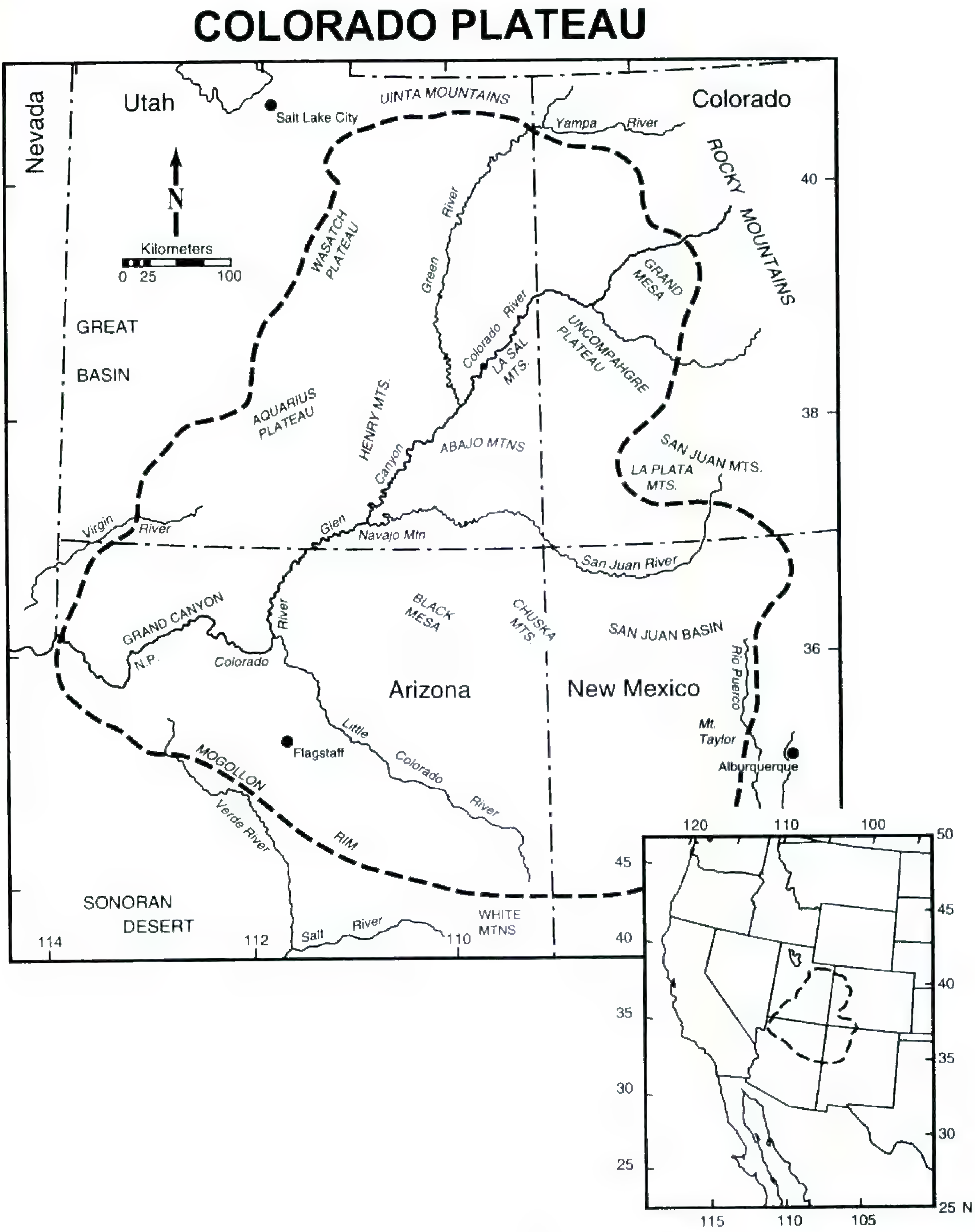

Figure 1. Boundary of the Colorado Plateau. For additional maps, articles, and photographs, see (http://www.cpluhna.nau.edu/index.htm).

1999a, 1999b). Although recent National Monument designations such as the Grand Staircase/Escalante have, in fact, taken into account the area's biodiversity and rich cultural heritage, these two factors have rarely been conceptually linked. More typically, they have been offered as "twin" attractions for ecotourists intrigued by redrock landscapes. Indeed, the 8 and 10 million tourists who annually visit national parks and monuments on the Plateau may receive some unanticipated exposure to this biodiversity and the ancient cultural influences upon it, but that is seldom what attracted

Table 1. National parks of the Colorado Plateau. Source: National Park Service website (http://www.nps.gov)

Park	State	Acreage
Arches	Utah	76,518
Black Canyon of the Gunnison	Colorado	27,705
Bryce	Utah	35,845
Canyonlands	Utah	337,597
Capitol Reef	Utah	241,904
Grand Canyon	Arizona	1,217,403
Mesa Verde	Colorado	52,121
Petrified Forest	Arizona	93,533
Zion	Utah	146,592
9 National Parks	2 in AZ; 2 in CO; 5 in UT	2,229,218 total acres (2.3 million acres)

them to the parks and monuments of the Painted Desert or Canyonlands in the first place.

Because about 13.5 percent of the Colorado Plateau's landmass is already protected by federal agencies, the ecoregion's extant biodiversity has not been considered as gravely imperiled as the biodiversity of other regions of North America. Nevertheless, our recent (unpublished) survey of more than 70 environmental professionals (including Native Americans) working on the Plateau indicates that this ecoregion remains unusually vulnerable to threats such as the damming of rivers; oil, gas, coal, uranium, and aquifer mining; competition from invasive species; mismanagement of wildfire regimes; and the fragmentation of wildland habitats by rapidly increasing urbanization. Such threats continue to diminish native biodiversity, both within and beyond national parks. The Nature Conservancy (TNC) has therefore ranked the Colorado Plateau within the third tier of hotspots of imperiled biodiversity. At the same time, TNC recognized that this ecoregion's "rarity-weighted species richness"

Table 2. National monuments of the Colorado Plateau. Source: National Park Service and Bureau of Land Management websites (http://www.nps.gov) and (http://www.blm.gov.)

Name	State	Managing agency	Acreage
Aztec Ruins	New Mexico	NPS	319
Canyon de Chelly	Arizona	NPS (leased from Navajo Nation)	83,840
Canyons of the Ancients	Colorado	BLM	164,000
Cedar Breaks	Utah	NPS	6,154
Colorado	Colorado	NPS	20,453
Dinosaur	Utah	NPS	210,277
El Malpais	New Mexico	NPS	114,277
El Morro	New Mexico	NPS	1,278
Grand Canyon-Parashant	Arizona	BLM	1,014,000
Grand Staircase-Escalante	Utah	BLM	1,900,000
Hovenweep	Utah	NPS	784
Montezuma Castle	Arizona	NPS	857
Natural Bridges	Utah	NPS	7,636
Navajo	Arizona	NPS (leased from Navajo Nation)	360
Pipe Spring	Arizona	NPS	40
Rainbow Bridge	Utah	NPS	160
Sunset Crater Volcano	Arizona	NPS	3,040
Tuzigoot	Arizona	NPS	40
Vermilion Cliffs	Arizona	BLM	293,000
Walnut Canyon	Arizona	NPS	3,579
Wupatki	Arizona	NPS	35,422
Yucca House	Colorado	NPS	33
22 National Monuments	10 in AZ; 3 in CO; 3 in NM; 6 in UT	BLM and NPS lands	3,859,549 total acres

was considered more significant and less well-known than it deserved to be (Stein et al., 2000); in other words, the Colorado Plateau harbors many biological rarities whose vulnerability to threats has not yet been adequately assessed. Consider the fact that the relatively well endowed Grand Canyon National Park has continued to lose an average of one species per year during the last two decades; the park's current research budget and resource management strategies have somehow not been sufficient to prevent the local extirpation of rare species.

Putting aside for the moment the degree to which current threats imperil the ecoregion's biota, it is clear that the Colorado Plateau is indeed rich in such rarities, including *endemic* species (that is, species with narrow distributions that occur in this ecoregion and nowhere else). Continent-wide floristic analyses by Kartesz and Farstad (1999) have affirmed that the Plateau is the ecoregion of continental North America with the highest rate of vascular plant endemism, reporting 290 species restricted to this ecoregion. For the fauna of the Colorado Plateau ecoregion, David Armstrong (in prep.) has recently determined that 23.6 percent of the mammals and 36 percent of the rodents exhibit endemism at the levels of species or subspecies.

While appreciation of the Plateau's biological uniqueness has grown, recognition of its cultural and linguistic uniqueness still lags far behind. The Colorado Plateau is home to more speakers of Native American languages than all other regions in the United States combined. The ecoregion's indigenous peoples belong to 24 different tribes, bands, or dialect communities and represent six different language families (Table 3).[1] (English, of course, as well as Spanish and Basque are also spoken here.) Among the Plateau's indigenous languages, Zuni is a language isolate, or what biologists might call an "endemic" language of the Colorado Plateau. According to many linguists, Zuni (*a:shiwi*) has no close relative in any other language family (Campbell, 1997). In addition to Zuni, the other language families indigenous to the Colorado Plateau include Keres, a family represented by Acoma Pueblo, Laguna Pueblo, and Zia Pueblo; Kiowa-Tanoan, the language family represented at Jemez Pueblo; Uto-Aztecan, the language family to which the Hopi, Ute, and Paiute languages belong; Athabaskan, represented by the Apache and Navajo languages; and Yuman, represented by the Yavapai, Havasupai, and Hualapai tribes on the Colorado Plateau. Figure 2 shows the approximate geographic boundaries of these six indigenous language families in 1850, when the Colorado Plateau officially became part of U.S. territory. Tribes and communities who spoke (speak) a language that belongs to one of the six families were living in these areas at that point in time. For example, Navajo and Apache speakers occupied the lands shown as "Southern-Athabascan" on this historical map.

The Colorado Plateau undoubtedly ranks among the top five American regions north of the Tropic of Cancer in terms of linguistic, cultural, and biological diversity, as well as in biological and linguistic/cultural endemism. Nevertheless, there is not a single conservation plan that takes into account both the cultural diversity and the biological diversity of the region. It is as if the historic and geographic relationships between "nature" and "culture" on the Plateau are somehow irrelevant, or too hotly debated to be of value in conservation planning. While it may be reasonable for conservation planners to be skeptical of painting all Native American land and water management practices as "ecologically noble," it is also tragic that so few Native American communities have been involved in planning national parks and monuments adjacent to their current reservations. These federal lands were clearly parts of their historic homelands (Burnham, 2000). As a result, the management of cultural resources and the management of natural resources have typically been done by different sets of specialists, sometimes involving Native Americans in the former but nearly always ignoring their traditional ecological knowledge of the latter.

This historic failure of the vast majority of conservation biologists and environmentalists to substantively engage Native American communities in collaborative work based on shared goals is both disappointing and ironic. It is ironic because the long-term residents of the Colorado Plateau have substantial knowledge about the history of the local flora and fauna that is not available from other sources. Even if all their current hunting, foraging, or farming practices are not considered to be ecologically benign by conservation biologists (Diamond, 1993), this does not negate the value of their traditional ecological knowledge (as defined by Berkes, 2000) about factors influencing plant and animal distributions, densities, and vulnerabilities. [Incidentally, Diamond's (1993) widely cited condemnation of prehistoric peoples of the Colorado Plateau for deforesting the Chaco Canyon area to obtain timber to build multi-storied pueblos has been refuted by recent strontium isotope evidence

[1] The numerous sources for Table 3 are found in the Literature Cited, and each source is preceded by an asterisk (*).

Table 3. Status of the Colorado Plateau's indigenous languages. Note: Sources for this chart are shown in the References section. Each source is preceded by an asterisk (*).

Tribe, band, or community	Total tribal landbase (acres)	Language or language subgroup	Language family affiliation	Total enrolled tribal members	Approximate percentage of fluent native speakers	Approximate percentage of fluent native speakers, ages 2–18
Jicarilla Apache	879,605	Apache	Eyak-Athabaskan	3,500	23%	<2%
Tonto Apache	85	Apache	Eyak-Athabaskan	110	30%	0%
White Mountain Apache	1,600,000	Apache	Eyak-Athabaskan	15,000	50%	13%
Alamo Navajo	63,000	Apache	Eyak-Athabaskan	2,000	95%	90%
Navajo Nation	17,000,000	Navajo	Eyak-Athabaskan	259,556	57%	<50%
Ramah Navajo	146,953	Navajo	Eyak-Athabaskan	2,463	60%	5%
Tóhajiileehé (Cañocito Band of Navajos)	80,000	Navajo	Eyak-Athabaskan	2,382	75%	50%
Havasupai	188,077	Pai	Cochimi-Yuman	639	98%	90%
Hualapai	1,000,000	Pai	Cochimi-Yuman	2,100	30%	<25%
Camp Verde Yavapai-Apache	636	Pai & Apache	Cochimi-Yuman & Eyak-Athabaskan	1,675	<2%	<2%
Yavapai-Prescott	1,395	Pai	Cochimi-Yuman	158	<2%	<2%
Kaibab Band of Paiute Indians	120,431	Southern Paiute	Uto-Aztecan	240	<2%	0%
Paiute Tribe of Utah	36,000	Southern Paiute	Uto-Aztecan	753	<2%	0%
San Juan Southern Paiute	5,000	Southern Paiute	Uto-Aztecan	300	75%	10%
Southern Ute	313,288	Ute	Uto-Aztecan	1,316	15%	5%
Uintah Ouray Ute	4,500,000	Ute	Uto-Aztecan	3,500	33%	<33%
Ute Mountain Ute	606,218	Ute	Uto-Aztecan	2,000	54%	2%
Acoma Pueblo	378,262	Western Keres	Keresan	6,344	50%	2%
Laguna Pueblo	491,387	Western Keres	Keresan	7,696	30%	2%
Hopi Pueblo	1,542,306	Hopi	Uto-Aztecan	10,916	48%	<8%
Hano (Hopi Tewa)		Tewa	Kiowa-Tanoan	600	65%	<2%
Jemez Pueblo	89,619	Towa	Kiowa-Tanoan	3,083	75%	50%
Zia Pueblo	117,000	Eastern Keres	Keresan	773	70%	<2%
Zuni Pueblo	463,270	Zuni	Zuni (no known relatives)	9,690	66%	60%
24 district tribes, bands, or communities in four different states	29,622,532	10 languages	6 language families	335,782		

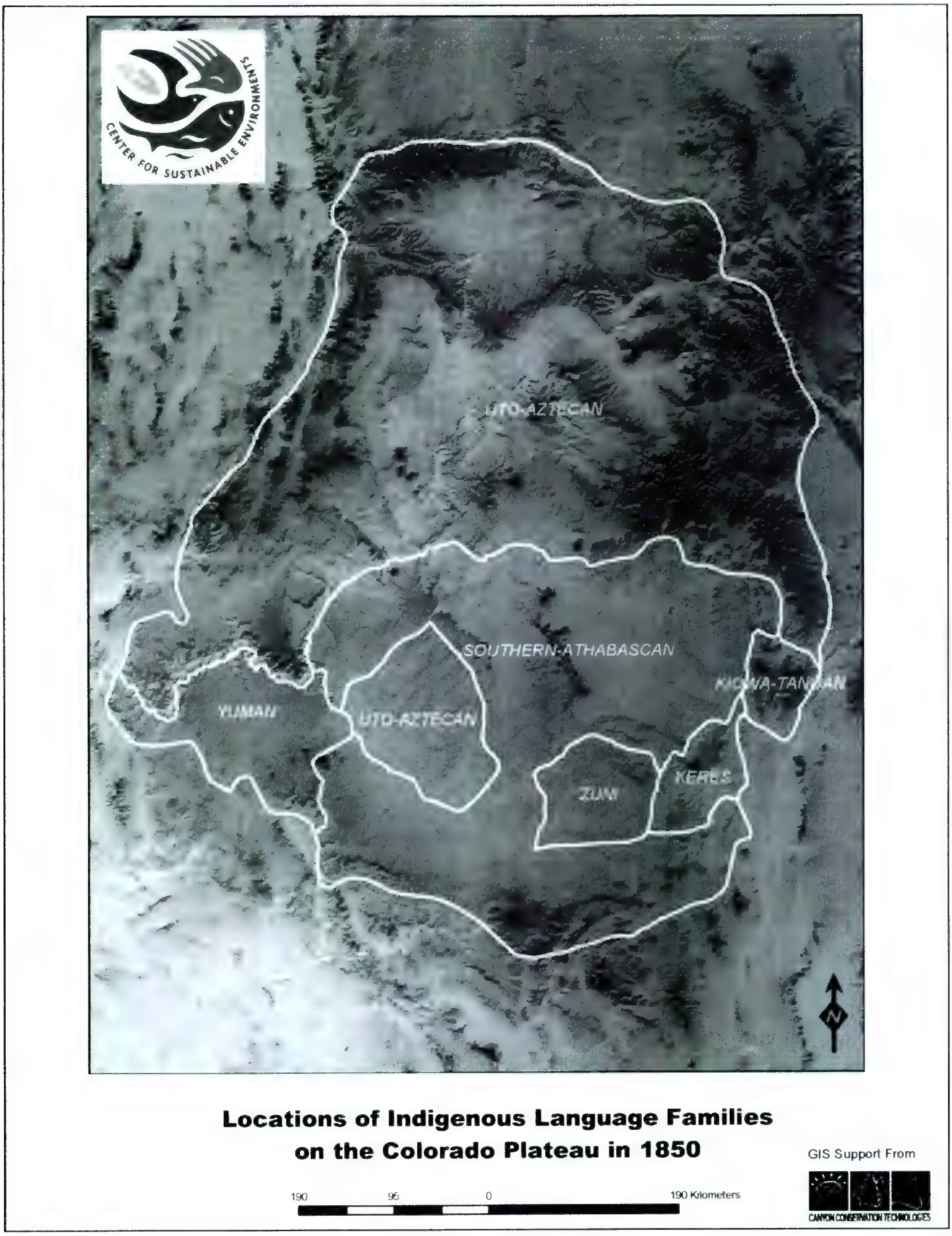

Figure 2. Locations of indigenous language families on the Colorado Plateau in 1850. (From data developed by the Center for Sustainable Environments.)

that the Chaco Anasazi obtained their ponderosa and spruce/fir beams by cutting a single age class of trees selected from two large mountain ranges 50–75 miles away (English et al., 2001).] Indeed, the more pertinent question is whether the traditional ecological knowledge of Plateau tribes is being lost at such a rapid rate that it will no longer be of service in biological conservation (Nabhan,

ligations (L. Masayesva Jeanne, in Nabhan & Reichhardt, 1983).

Traditional ecological knowledge can also be useful in locating and staging rare species reintroductions and habitat restoration. At a time when the California Condor recovery efforts in California were on the verge of failure, Rea (1981) proposed that the recovery team broaden its view and consider reintroductions in the historic refugium near the Colorado River's Grand Canyon, where oral histories from the Hopi recall sightings of the giant bird they call *kwaatoko* (Whiting unpublished, in Seaman, 1993). This has, in fact, turned out to be one of the more successful areas for Condor reintroduction, even though it is outside of California where many biologists erroneously presumed that the California Condor belonged (Rea, 1981).

Investment in Conservation Capacity-Building for Native Americans Remains Critical

For decades, the Bureau of Indian Affairs hardly involved Native Americans in so-called technical decisions regarding biological resource and land management options on tribal lands. While the number of Native Americans trained in biology and nature resource management increased fivefold between 1970 and 1999, there remains a chronic underinvestment in training Native American professionals in biodiversity conservation on tribal lands relative to the training available for professionals managing federal lands. The Navajo Natural Heritage Program, first sponsored by The Nature Conservancy, has become an outstanding example of the "conservation pay-off" of such investment (Stein et al., 2000). The Hopi, Zuni, and White Mountain Apache tribes have also developed programs that include wildlife management, endangered species recovery, and ecological restoration. In the case of the Zuni, their program to reintroduce beavers as part of the tribe's riparian restoration efforts has involved elders teaching youth about the cultural significance of beavers and other wetland dwellers (Albert & Trimble, 2000). When both Western academic and traditional ecological knowledge are valued by such programs, it ensures that Indian youth interested in natural history are not forced to choose between their own cultural way of looking at the natural world, and the way of modern science. One superlative example of such capacity-building efforts among Native Americans is the EPA-funded Institute for Tribal Environmental Professionals based at Northern Arizona University, which has already trained more than 500 tribal members from over 200 communities in inventory, monitoring, and restoration techniques for environmental protection.

More Linkages Are Needed Between Ecological Restoration and Linguistic Revitalization

In addition to the many ecological restoration projects recently initiated on tribal lands, most Native American communities on the Colorado Plateau are actively engaged in language stabilization and revitalization efforts (Cantoni, 1996). These language restoration projects often include the elaboration of the entire extant lexicon of a tribe, including its names for plants, animals, and their habitats. In eliciting these names, linguists often do not know the particular scientific taxa the words are describing, but nevertheless record ecological information that may be of use to ecological restoration and species recovery projects (Nabhan, 2000a). For instance, the Diné name for the Indian paintbrush, *Castilleja lanata* A. Gray, is *dah yiitihidaa tsoh*, meaning "big hummingbird's food," to distinguish it from the beardtongue, *Penstemon barbatus* (Cav.) Roth, called *dah yiitihidaa'ts'ooz*, or "food of the slender hummingbird." It may be that Diné elders recognize that these two flowers are frequented by different sizes and species of hummingbirds, and that such information can be integrated into ecological restoration efforts to increase forest understory biodiversity.

Conclusions: Implications for Global Conservation Strategies

Over the last decade, tremendous effort has gone into defining, locating, and rapidly assessing the species richness of "hotspots of biodiversity" (Mittermeier et al., 1998; Olson & Dinerstein, 1998; Ricketts et al., 1999a). By some accounts, these hotspots not only capture a large proportion of the planet's biodiversity, but they also define an agenda for conservation investment, which is largely expended on land purchases and infrastructure development for protected areas (Mittermeier et al., 1998). By investing an average of $40 million/year on land purchases in hotspots, rather than on the current "scattergun" approach of current conservation expenditures, these conservation strategists have proposed a new "silver bullet" to biodiversity loss that could protect areas containing a high proportion of the world's species, while business outside the hotspots could be allowed to go on as usual.

Ehrenfeld (in press) has pointed out the serious

2000a). To date, this rapidly disappearing orally transmitted knowledge has rarely been systematically taken into account and valued by land managers, who often consider such knowledge to be the quaint but anecdotal or superstitious recollections of scientifically untrained old-timers.

Even contemporary Native Americans' roles in managing the lands of the Colorado Plateau have been chronically underestimated. While the Grand Canyon Trust considers "Indian country" to comprise just a quarter of the Colorado Plateau's 130 million acres (Hecox & Ack, 1996; Wilkinson, 1999), our GIS-based analyses more accurately establish that 29–32% of the Colorado Plateau is being managed by Native American communities (depending upon which definition of the Plateau's boundaries is used). By virtue of this fact alone, it would be presumptuous if not impossible to develop a systematic conservation plan for this ecoregion that did not take into account Native American land stewardship and traditional ecological knowledge of endangered species on the Colorado Plateau (Nabhan, 2000a, b).

In a modest effort to begin to bridge the historic gap between studies of biological and cultural diversity, Northern Arizona University's Center for Sustainable Environments (CSE) has initiated a pilot study with the Grand Canyons Wildlands Council to assess ways to better safeguard and restore both the biological and the cultural uniqueness of the Colorado Plateau. In designing this pilot study, we have investigated the potential linkages between biological and linguistic diversity elucidated by the scholars involved in "Terralingua: Partnerships for Linguistic and Biological Diversity," an international non-profit organization hosted by CSE, which has recently published a global analysis of biocultural diversity (Maffi, 2001). The following discussion emphasizes why efforts to conserve biological and linguistic diversity should be linked, whenever possible, using examples from the Colorado Plateau.

The Biodiversity on Native American Lands Deserves More Conservation Investment

Indian reservations in the United States cover tens of millions of acres of the North American continent, comparable in extent to the acreage that the National Park Service manages for North America's biodiversity. In particular, reservation lands on the Colorado Plateau (Fig. 3) cover nearly twice the area that national parks, monuments, preserves, conservation areas, wilderness areas, and wildlife refuges cover in the same ecoregion. Nevertheless, the 29.6 million acres of lands managed by Native Americans on the Colorado Plateau have yet to receive much investment from federal or private sources for the inventory of their biodiversity, monitoring, and recovery of their rare species, or local capacity-building in environmental protection—relative to the considerable support given to those working on adjacent federally protected lands.

If all the species found on Indian lands were also found on lands rigorously protected by the National Park Service or The Nature Conservancy, perhaps this issue would be easier for conservation biologists to ignore. However, the narrowly distributed endemics of the region are often restricted to habitats found only on reservation lands, and not on park lands. The Navajo sedge, *Carex specuicola* J. T. Howell, is an endangered species found around only three springs and seeps used by Diné (Navajo) livestock herders, and one spring used by Hopi farmers. In other words, its range is restricted to the Navajo and Hopi Reservations (D. House, pers. comm.; Nabhan et al., 1991). Similar situations occur for the endemic Hopi chipmunk (*Tamias rufus*), a subspecies of the Spotted Ground Squirrel (*Spermophilus spilosoma cryptospilotus*), the Chuska and Tunitcha Mountain subspecies of Abert's squirrel (*Sciurus aberti chuskensis*), and a subspecies of Stephen's woodrat (*Neotoma stephensi relicta*) found only on Navajo lands. Even if conservation biologists continue to feel ill-equipped to deal with the cultural and legal (sovereignty) issues regarding plants and animals restricted to tribal lands, they can no longer ignore the fact that the only means to sustain these species is by providing Native American land managers with the resources needed to protect or recover these rare populations and their habitats.

The Conservation Community Needs to Embrace Traditional Ecological Knowledge

Until recently, endangered species recovery teams and ecological restorationists disregarded the traditional ecological knowledge found in Native American communities. Perhaps the first formal breakthrough occurred when Diné biologist Donna House incorporated traditional ecological and ethnobiological knowledge about the Navajo sedge into its federal species recovery plan (House in Nabhan et al., 1991), acknowledging that Diné herders had been stewards of this plant's habitat for decades and deserved to participate in further efforts to safeguard the sedge.

In addition to their role as habitat managers, some cultural communities on the Colorado Plateau intentionally protect rare species, as is the case

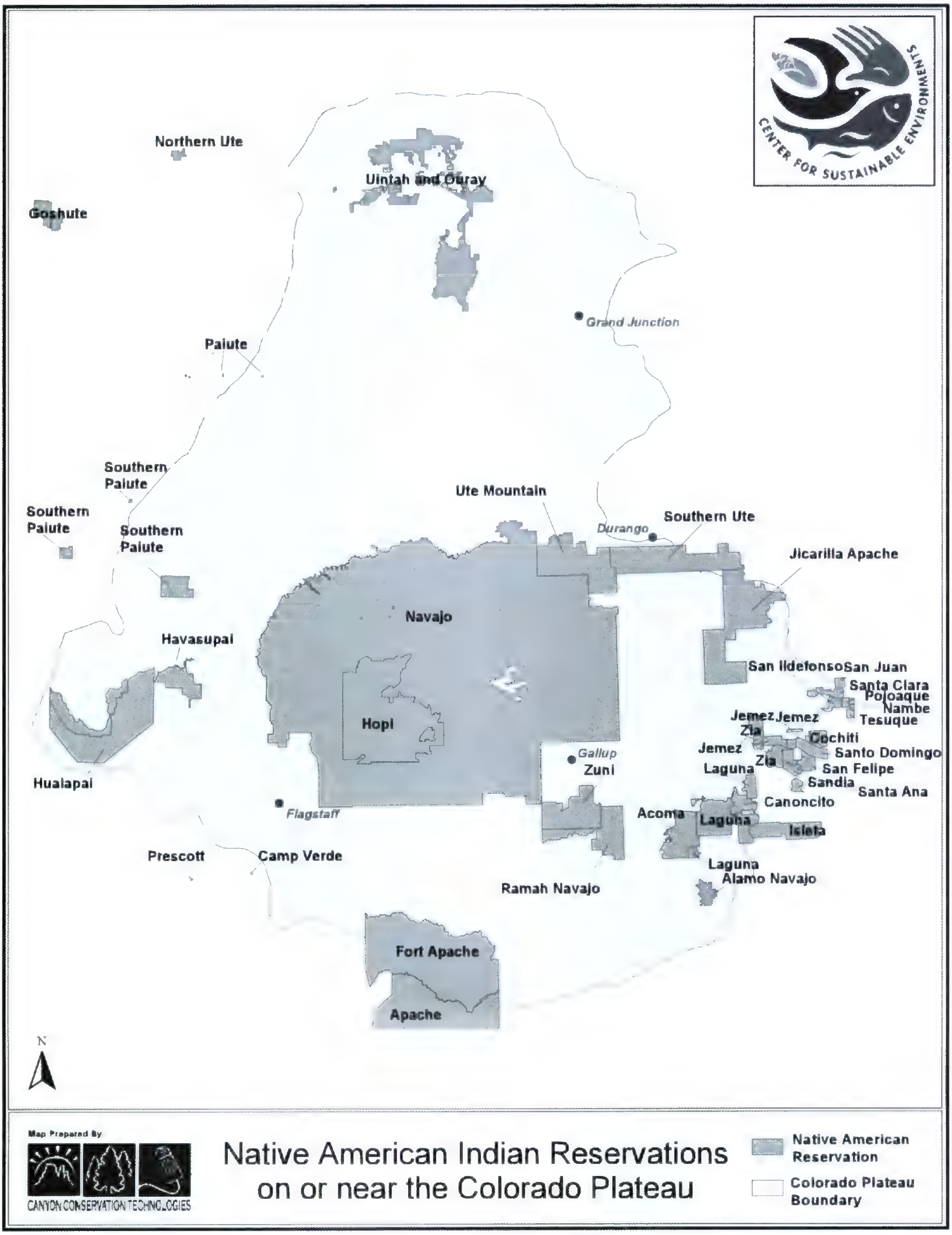

Figure 3. Native American Indian Reservations on or near the Colorado Plateau.

with the anomalous sunflower (*Helianthus anomalus* S. F. Blake). Of the twenty-five known localities for this species, at least seven are in or adjacent to Hopi fields and kivas, where farmers and priests spare it from their otherwise rigorous weeding practices (Nabhan & Reichhardt, 1983). Its flowers may be the sole source of a ceremonial facepaint prepared for the *Lakon mana* (maiden) ceremonies of early fall, so that these sunflower populations are protected as a necessity for fulfilling spiritual ob-

flaws associated with such an agenda, the most serious being that most hotspots are not only inhabited by diverse cultures, but they are also not for sale. By the mid 1990s prominent ethnobiologists, anthropologists, linguists, and biogeographers had brought attention to the fact that the 10–20 richest biodiversity hotspots were also extremely rich in cultural diversity, which was typically defined in terms of the richness of extant indigenous languages (Harmon, 1995). For instance, Toledo (1994) observed that of the nine countries considered to have the highest species richness of mammals, six of these were also among the richest in indigenous language groups: Indonesia, Brazil, Mexico, Zaire, India, and Australia.

Three commentaries are typically offered to explain this correlation and to hypothesize its causes (as cited by various authors in Maffi, 2001):

- *Geographic determinism*: Both species and languages diversify in heterogeneous landscapes with formidable geographic barriers.
- *Ecological determinism*: Linguistic diversification occurs in response to high biodiversity, as different cultural groups explore diverse ecological niches for themselves and encode their knowledge of rich biotas in different ways.
- *Historic determinism*: Areas of high linguistic diversity today are "residual," persisting because of their geographical isolation from extensive agricultural development (implying that now-impoverished areas were once more diverse).

Clearly, our Colorado Plateau pilot study reiterates a pattern seen on other continents as well: where hotspots of biodiversity or endemism are inhabited by a diversity of cultures, the ways in which these cultures encode traditional ecological knowledge about species in their native languages has tremendous potential for helping to conserve this biodiversity (Nabhan, 2000b). From this frequently observed correlation, several management implications must be considered:

- It may not be feasible or even advisable for government or non-government organizations (NGOs) to purchase the lands within these hotspots for biodiversity protection, because much of the biologically diverse area may be "common lands" held in trust by these cultural communities, such that they cannot be purchased, traded, or condemned. New efforts to conserve biodiversity elsewhere in the world need not make the same mistake the National Park Service historically made on the Colorado Plateau, by stealing, condemning, or finagling the rights to species-rich lands held in trust for future generations of indigenous peoples (Burnham, 2000).
- It is probable that for such high levels of biodiversity to persist in any hotspot until this day, indigenous residents consciously or unconsciously developed active and passive means of managing particular landscapes, microhabitats, or species guilds to maintain them. The potential utility of such knowledge, skills, and practices is great (Nabhan, 2000b), so much so that species recovery teams and formal land managers should be encouraged to integrate such knowledge into their conservation management plans (Tuxill & Nabhan, 1998).
- It is likely that proponents of biodiversity conservation will forge stronger, more effective collaborations with indigenous residents in biodiversity hotspots if they listen to and respect indigenous concerns about sovereignty, cultural property rights, and secrets associated with esoteric beliefs and ceremonies. Conservationists should attempt to collaborate on community-based projects that foster the continued oral transmission of traditional ecological knowledge, the persistence of indigenous languages, traditional subsistence or ceremonial practices, and the generation of health benefits or income for a broad cross section of community members. While such community-based conservation efforts are already given lip service from governments and NGOs alike, there remains a disproportionate investment in "top-down" conservation strategies and only scattered investment in community-based "bottom-up" strategies for maintaining biodiversity.
- Given the fact that traditional ecological knowledge about landscape-level biodiversity itself is being diminished (Berkes, 2000), the fragile relationship between the two needs to be more tangibly explored. While many biogeographers and linguists are already involved in efforts to understand global patterns of biodiversity and cultural diversity, it is hoped that our pilot project to safeguard the uniqueness of the Colorado Plateau will encourage other community-based practitioners to experiment with more practical means of integrating indigenous knowledge into collaborative efforts to conserve the world's hotspots of diversity and endemism.

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⟨http://www.earizona.com⟩ [Camp Verde Yavapai-Apache]
⟨http://www.yavapai-apache-nation.com⟩ [Camp Verde Yavapai-Apache]
⟨http://www.dced.state.ut.us/indian⟩ [Paiute Tribe of Utah]
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⟨http://www.swr.-hq.nm.bia.gov/99ABQIf.htm⟩ [Bureau of Indian Affairs: "Southwest Region Combined Totals"]
⟨http://www.indigenous-language.org⟩ [Indigenous Languages Institute, Santa Fe, New Mexico: "Endangered Languages Database." Accessed 5 December 2001]

THE UNITED STATES NATURALIZED FLORA: LARGELY THE PRODUCT OF DELIBERATE INTRODUCTIONS[1]

Richard N. Mack[2] *and Marianne Erneberg*[3]

Abstract

Over the past 400 years plant immigrants have arrived in the United States in huge numbers, the results of accidental and deliberate introduction by humans. Very few immigrations, however, result in naturalizations; the environmental hazards for immigrants in a new range are usually acute and chronic. We traced the history of introduction among the naturalized taxa within a group of U.S. regions and states that span much of the environmental amplitude of the United States. Despite differences among these regions in physical environments and the length of their histories of plant immigration, the proportion of their naturalized floras that likely arrived through deliberate introductions is greater than 50 percent. Many of the first species to become naturalized in the northeastern United States were introduced as food seasonings or putative sources of medicine. Erstwhile ornamentals are prominent components of all the naturalized floras, especially in Florida. Some species introduced as sources of forage or fiber also became naturalized. Before 1900 many now naturalized species were introduced repeatedly and widely into the United States as seed contaminants through an extensive international commerce in crop seeds. The mode of entry is unknown for approximately 30 percent. The likelihood that the majority of species now naturalized in the United States has a history of deliberate introduction and post-immigration cultivation provides a plausible explanation for their persistence in a new range.

Key words: biotic invasion, environmental stochasticity, naturalization, ornamentals, seed catalogs, seed contaminants.

Comparisons of the sizes of regional naturalized floras with the total number of species that have likely arrived in these new ranges produce a commonly shared conclusion: few immigrant species ever become naturalized (sensu Mack et al., 2000). Williamson (1993) argued that this difference in the number of immigrant species, the number that reside temporarily (adventive or casual species), and the number that subsequently become naturalized differ in turn from each other by an order of magnitude. Accurate determination of these proportions is rarely possible (but see Holdgate, 1964). Nevertheless, the discrepancy between the number of species that arrive in a new range and the number that eventually persist appears huge (Williamson & Fitter, 1996). Today more than 30,000 plant taxa are commercially available in Australia (Hibbert, 1999), even more in the United States (Isaacson, 1996); most are routinely cultivated outside glasshouses or other shelter. Yet even liberal estimates put the total size of the naturalized flora for each country at less than 3000 species (Hnatiuk, 1990; Kartesz, 1994).

Pursuit of explanations for the long odds against naturalization that confront immigrant species have long attracted the attention of biologists (de Candolle, 1855; Gray, 1879) because any general explanation would aid substantially the prediction of which non-indigenous species will persist. This fascinating topic in ecology and biogeography has recently taken on added importance as nations grapple with erecting legally defensible scientific

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protocols by which they may exclude harmful non-indigenous species (Glowka & de Klemm, 1999). Despite numerous attempts to identify the few that will become naturalized among a host of immigrant species (e.g., Rejmanek & Richardson, 1996; Reichard & Hamilton, 1997), we still lack a general explanation for this numerical discrepancy, much less a predictive protocol (Williamson, 1999).

Explanation lies in a better understanding of the interaction between immigrants and the environment in a new range. All populations are subjected to multiple, random environmental events and circumstances, whether in their native or new range (Simberloff, 1988). The consequences of random detrimental events, e.g., prolonged or acute drought or frost, sudden and massive attack by predators or virulent parasites, are particularly devastating for small populations. Although the sheer size of a large population provides some numerical buffering from repeated losses of a percentage of its members, the same percent losses for a small population can rapidly bring it to extinction, unless members are replaced through reproduction or immigration, or both (Menges, 1992, 1998). Many, and perhaps most, immigrant populations are small founder populations for which there is no likelihood that individuals will be added through recurring immigration. The randomly occurring losses caused by ubiquitous environmental stochasticity can readily prove dire (Mack, 1995). Thus, even for an immigrant population with attributes that allow it to tolerate the average expression of conditions in a new environment, it could still be destroyed by the chance, repeated occurrence of extreme environmental events (Crawford, 1989; Crawley, 1989).

The *raison d'être* for cultivation is the deliberate protection of plant populations from environmental hazards, including those with stochastic expression. Such protection can allow the population to reach a numerical threshold, such that it can sustain losses arising from subsequent stochastic events. At that threshold size the population may become naturalized, even if cultivation is withdrawn. Thus, cultivation emerges as a potential counter-force to environmental stochasticity and may well facilitate naturalization (Mack, 2000).

If there is a causal link between cultivation and plant naturalization, we hypothesized that there should be a corresponding correlation between cultivation and the history of those species that have become naturalized. For example, in any naturalized flora, the majority of species should have a history that includes cultivation upon entry into the new range. Clearly, some species have no such link; immigrants could arrive in a new range and become naturalized without human dispersal or cultivation (e.g., Ridley, 1930; Mack & Lonsdale, 2001). If our hypothesis is correct, these examples would, however, form a minority of naturalizations.

To test our hypothesis we investigated the mode of pre-1900 introduction among the naturalized species within a group of continental U.S. floras and compared this evidence with similarly constructed tallies for naturalized floras from South Australia (Kloot, 1987), Hawaii (Wester, 1992), and northern Europe (Weidema, 2000). Time to naturalization can vary substantially (Mack et al., 2000). We attempted to circumvent most uncertain cases of naturalization by restricting our investigation to species that had arrived in the United States before 1900. As a result, their status as naturalized is based on at least 100 years of residence in the United States.

Methods

We recognized that our investigation could be complicated and handicapped by the sometimes conflicting synonymy of binomial names across the last two centuries and differences among floras in the definition of naturalized species. We selected published U.S. floras or checklists that identify naturalized species as those that persist without aid of recurring human cultivation; furthermore, these floras clearly make a distinction between adventive (temporary, waif, transient) species and naturalized species. Our selection criteria are met by recent floras or checklists for New York (Mitchell, 1986), Rhode Island (Gould et al., 1998), Florida (Wunderlin, 1998), and North-Central Texas (Diggs et al., 1999). We did, however, delete 46 species that Wunderlin (1998) considered naturalized because he reported that each of these species has been collected only once or has not been collected recently. We employed Fernald's (1950) *Gray's Manual of Botany*, 8th ed., because of its coverage of the northeastern quarter of the United States, a region with diverse habitats, and its frequent descriptions on the mode of introduction for non-indigenous species. These floras collectively represent much of the diversity within the continental U.S. naturalized flora.

We attempted to determine the history of introduction for each naturalized angiosperm in these floras. We deliberately excluded other plant groups from our study as the records for some of these groups (e.g., cryptogams) are much less complete and reliable. Information is rarely collected on a species' introduction event(s), although some introductions can be traced in detail (e.g., Haughton,

Table 1. Summary of the likely mode of entry (deliberate, seed contaminants, as both deliberate & seed contaminants, and unknown) for angiosperm species now naturalized in Florida, north-central Texas, the central northeastern United States, Rhode Island, and New York as derived from published floras (see footnotes 1–5). Numbers in all but the last column are the percentages of the total naturalized flora that arrived by a mode of introduction.

	Delibrate introductions	Seed contaminants	Deliberate & seed contaminants	Unknown	Number of taxa
Florida[1]	67	1	1	31	1161
North-central Texas[2]	62	2	3	34	417
Central northeastern United States[3]	59	3	3	35	559
Rhode Island[4]	59	3	3	35	408
New York[5]	57	3	4	37	391

[1] Wunderlin (1998).
[2] Diggs et al. (1999).
[3] Fernald (1950).
[4] Gould et al. (1998).
[5] Mitchell (1986).
Sources for the modes of introduction: Anon. (1882), Austin (1978), Bailey (1906), Barton (1818), Blake (1922), Coon (1974), Darlington & Wylie (1955), Darlington (1826), Darlington (1859), Darwent & Coupland (1966), de Schweinitz (1832), Diggs et al. (1999), Duke (1985), Faden (1989), Fernald (1950), Fernald & Kinsey (1943), Ferreira et al. (1997), Gordon & Thomas (1997), Grieve (1959), Haughton (1978), Hitchcock (1950), Howell (1959), Hume et al. (1983), Josselyn (1672), Lamson Scribner (1869), le Strange (1977), Long (1922), McCarthy (1888), McCartney (1984), Mack (1991), Mahler (1980), Mohr (1878), Morton (1976), Morton (1989), Muenscher (1955), Oakley & Westover (1916), Old (1981), Piper (1915), Pursh (1814), Rhoads & Klein (1993), Ridley (1930), Schery (1965), Schmitz et al. (1991), Smith (1900), Spencer (1984), Stillé & Maisch (1880), Sturtevant (1919), Tanaka (1976), Uphof (1968), Weldon et al. (1969), Wunderlin (1998).

1978; Mack, 1991; Schmitz et al., 1991, and references therein). In the absence of contemporaneous records of a species' introduction, we established criteria for identifying the most plausible introduction scenario. Species considered here to have arrived through deliberate introduction have a history of pre-1900 human use within the species' native range or in the United States. We reasoned that if a species had been used for centuries as, for example, a seasoning or herbal in western Europe (Sturtevant, 1919; Grieve, 1959), it was likely introduced deliberately by human immigrants to the United States (e.g., *Nepeta cataria* L., *Dipsacus fullonum* L., *Taraxacum officinale* Weber).

Crop seeds have been imported to North America by Europeans for more than 400 years (Viola & Margolis, 1991). Throughout most of this time seed cleaning has been either not practiced, ineffective, or even subverted (see Discussion); consequently, arriving as a seed contaminant became a likely accidental mode of entry for some species. Species were considered to have arrived by this mode if they had a pre-1850 history as seed contaminants in Europe or the United States (e.g., de Schweinitz, 1832).

For many species a pre-1900 record of use is recorded in herbals and horticultural compendia (e.g., Bailey, 1906; Fernald & Kinsey, 1943; Grieve, 1959; Uphof, 1968), plant *materia medicas* (Stillé & Maisch, 1880), pre-1860 U.S. floras (e.g., Pursh, 1814; Darlington, 1859), and 19th century state and federal agricultural publications (see footnotes in Table 1). In addition to the primary literature, we searched 19th century seed catalogs that had been distributed in the eastern United States (Mack, 1991, and references therein). These catalogs not only report a large array of non-indigenous species for sale, but most also state each species' binomial name and uses (Appendix 1). Fernald (1950), Wunderlin (1998), and Diggs et al. (1999) indicated a mode of introduction for some species, and their determinations supplemented our other sources.

We initially searched in the pre-1900 literature for species under their currently accepted names. Fortunately, many plant species names have been retained since their initial description [e.g., *Rumex crispus* L., *Stellaria media* (L.) Vill.], although we usually cannot verify the species' identification in a historic account. Some naturalized species in the modern floras were left without an assigned mode of introduction because we could not reliably identify them in the 19th century literature. These were placed in the Unknown Category. The state or regional floras from which we prepared our tallies all include some naturalized subspecies and varieties. We usually could not identify these taxa within the pre-1900 botanical literature, and unidentified taxa

were also assigned to the Unknown Category. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Results

Results of our investigation of the history of introduction among these naturalized floras are summarized in Table 1. (Only this summary is provided here. Information on the mode of introduction for each investigated species is available from the authors upon request.) The majority of angiosperm species within each naturalized flora has a pre-1900 history of use in their native range or the United States, or both. The percentage of such deliberate use is similar among the floras: lowest within the New York flora (57%), highest in the Florida flora (67%). Some species have both a history of use and were 19th century seed contaminants (e.g., *Agrostemma githago* L., *Bromus secalinus* L., *Centaurea cyanus* L., *Convolvulus arvensis* L., *Ranunculus acris* L.) (de Schweinitz, 1832; Fernald, 1950; Grieve, 1959; Haughton, 1978; Mack, 1991). These species, which form 1 to 4% of the naturalized angiosperm floras, are recorded in Table 1 as both intentional and accidental introductions. The total percentage of these naturalized floras with a post-immigration link to cultivation, introduced either deliberately or as contaminants in crop seeds, is between 64 and 69%. The modes or circumstances under which the remainder (31–37%) arrived in their new U.S. range are unknown.

Similarity in the percentages among the floras surveyed for the central northeast United States (Fernald, 1950), Rhode Island (Gould et al., 1998), and New York (Mitchell, 1986) is due in part to the similarity of these three species lists. Differences do occur, however, and may reflect the 40- to 50-year differences in the collection spans between Fernald (1950) and the other two accounts, as well as differences in the intensity of collection. Florida's climate and less intense pattern of human settlement until the 20th century (Gannon, 1996) has yielded a naturalized flora that is largely not represented elsewhere in the conterminous United States. Most of its naturalized species have subtropical or tropical native ranges (Wunderlin, 1998), and many of these species were imported for potential use as ornamentals and maintained in government test gardens (Gordon & Thomas, 1997). This intensity of plant introduction for ornamental horticulture perhaps explains the high percentage (69%) of its naturalized flora that has a post-introduction link to cultivation.

Discussion

Our results reveal a strong correspondence between naturalized species and these species' deliberate introduction and cultivation (Table 1). Other species that arrived as seed contaminants in crop seeds would have been the collateral beneficiaries of cultivation. Together, the proportions in these two categories support the contention that cultivation, whether deliberately or inadvertently supplied for an immigrant species, could have contributed to the persistence of at least 60 percent of the naturalized angiosperm species in the regions we assessed.

The fate of deliberately introduced species

The major agent for spreading plants into new ranges around the globe for at least the past 400 years has been human immigration. In embarking on an oceanic voyage of colonization, all peoples, whether Polynesians and Melanesians across the Pacific (Whistler, 1991) or Europeans worldwide (Mack, 1999, 2001), have carefully ensured that they carry their domesticated plants with them. This motivation springs from a deep-seated need to anticipate and resolve the dilemma caused by unknown, uncertain, or at least not assured sources of food, fiber, forage, and other essential plant products in a new range. Even if would-be colonists had advance knowledge that indigenous species in their new homeland could sustain them, plans for transoceanic colonization have carefully included the transport of the germplasm of essential crops in the initial voyage. Invariably, this transfer of species that were deemed desirable, if not essential, has been maintained long after the colony's survival was assured (Mack, 1999, 2001).

The rapidity with which the early colonists in eastern North America established European crops is remarkable; dire necessity is indeed a powerful stimulus. Tuckerman (see Josselyn, 1672) cited an account by Higginson in 1629 in which he raved about the vigor and diversity of the European crops already available in New England, including beets, carrots, cabbage, asparagus, radishes, and lettuce. From the standpoint of species that were to become members of the naturalized flora, Higginson's list of introduced herbs is revealing: sorrel, parsley, chervil, and marigold for pot-herbs, along with sage, thyme, clary, anise, fennel, coriander, spearmint, and pennyroyal as "sweet herbs."

Cultivated fields and gardens with these European species produced some of the earliest naturalized species in North America. By 1672 Josselyn reported seeing "Dandelion" (*Taraxacum officinale* Weber), "Wormwood" (*Artemisia absinthium* L.),

and "Black henbane" (*Hyoscyamus niger* L.) growing outside cultivation in New England. A century later, Kalm (1770) found other species, including *Tanacetum vulgare* L. and "Datura" (*Datura stramonium* L.), that had also escaped cultivation.

The diversity of species used for medicinal purposes and as seasonings (Grieve, 1959) likely provided the largest single array of species naturalized in the United States by ca. 1800. Of the 559 species listed by Fernald (1950) as naturalized, at least 65 were in use before 1900 as herbal remedies or seasonings. Early 19th century seed catalogs often contained sections devoted to "pot-herbs" and medicinal species: many of the species in these lists are now naturalized throughout the United States (Mack, 1991). As suggested in Josselyn's (1672) list, it is likely that many of these species had been introduced much earlier. By the early 19th century some were already being listed as naturalized in regional floras, such as *Anthemis cotula* L., *Cynoglossum officinale* L., *Inula helenium* L., *Nepeta cataria* L., *Solanum nigrum* L., *Solidago odora* Ait., and *Urtica dioica* L. (Barton, 1818). In addition, Pursh (1814) noted the persistence of *Cannabis sativa* L. ("*Cannabis sativa*"), *Cichorium intybus* L. ("*Cichorium intybus*"), *Conium maculatum* L. ("*Conium maculatum*"), *Hypericum perforatum* L. ("*Hypericum perforatum*"), *Linum usitatissimum* L. ("*Linum usitatissimum*"), *Marrubium vulgare* L. ("*Marrubium vulgare*"), and *Ricinus communis* L. ("*Ricinus communis*"). Forage grasses, an early perceived deficiency within the native flora, were also actively imported (Cronon, 1983). As a result, western European pasture species were members of the pre-1800 naturalized flora: *Aira praecox* L., *Holcus lanatus* L., *Lolium perenne* L., *Phleum pratense* L., *Poa compressa* L., *Poa annua* L., *Poa pratensis* L. (Barton, 1818).

European fruit trees were planted very early in the settlement of New England (Young, 1846). By 1671, quince, apple, pear, cherry, damson [*Prunus domestica* var. *insititia* (L.) Fiori & Paoletti], plum, and common barberry were all commonly grown (Josselyn, 1672). Several of these species [*Prunus avium* (L.) L., *Malus pumila* Mill.] have become naturalized but appear innocuous. However, common barberry's introduction was soon to plague the colonists. *Berberis vulgaris* L. is a host for *Puccinia graminis* f. sp. *tritici*, the stem rust of wheat, and it would be almost three centuries before common barberry was controlled effectively in the United States (Anon., 1937).

Ornamentals, i.e., species introduced purely for aesthetic reasons, were introduced surprisingly early, given the colonists' need to first establish reliable sources of food, fiber, forage, and medicine. By 1672 Josselyn was commenting on the imported ornamentals (lavender cotton, hollyhocks, satin, gillyflowers, pinks, English roses, and eglantine) that he encountered in New England. Eglantine (*Rosa eglanteria* L.) is now naturalized in the United States (Fernald, 1950). Given its early introduction, it may be one of the first European ornamental species to become naturalized in the United States. In introducing ornamentals, the colonists were greatly expanding the taxonomic breadth and geographic range from which naturalized species would be drawn. We lack adequate records of the market in ornamental species that emerged in the 18th century. However, Cutler (1785) reported matter-of-factly that seeds of an *Antirrhinum* species were imported by seed-sellers in New England, and a broadside of "Garden and Grass Seeds, with a choice collection of Flower Roots, & Seeds, Just Imported" was produced as early as 1793 in Richmond, Virginia (National Agricultural Library archives, as cited in Pennsylvania Horticultural Society, 1976).

With the apparent proliferation of seed catalogs by 1800, scores of species were arriving in the United States from a worldwide list of native ranges. Ornamental species (and earliest date of their appearance in a seed catalog published in the United States) include *Lonicera japonica* Thunb. (1823), *Lantana camara* L. (1804), *Melia azedarach* L. (1807), *Mesembryanthemum crystallinum* L. (1807), *Mimosa pudica* L. (1804), *Myrica faya* Dryand (1823), *Rhamnus cathartica* L. (1807), *Rosa multiflora* Thunb. (1826), *Schinus terebinthifolius* Raddi (1832), and *Ulex europaeus* L. (1807) (Mack, 1991). By 1804 a Philadelphia seed merchant could describe himself as someone who had for sale, ". . . an extensive variety of Asiatic, South-Sea Islands, African, and European Seeds, of the most curious and rare kinds; and is daily adding to his collection, as he avails himself of every opportunity to procure seeds from all parts of America, as well as from every part of the world, to which the enterprise of American commerce extends . . ." (B. M'Mahon [1804: 1] "A catalogue of American Seeds . . ."; archives of the National Agricultural Library, Beltsville, Maryland). The speed with which regions only recently colonized by Europeans were contributing species to this global traffic in ornamental plants is impressive. D. & C. Landreth, seed merchants in Philadelphia, offered nine *Melaleuca* species from "New Holland" (Australia) in their 1832 catalog (archives of the Pennsylvania Horticultural Society, Philadelphia). In all likelihood, these species had been imported even earlier

Table 2. Naturalized species in the United States considered by de Schweinitz (1832) to have been deliberately introduced. Some of the names employed by de Schweinitz are not in current nomenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Agrostis gigantea Roth. (*Agrostis alba*)	*Plantago major* L. (*Plantago major*)
Agrostis tenuis Sibth. (*Agrostis vulgaris*)	*Poa pratensis* L. (*Poa pratensis*)
Anthoxanthum odoratum L. (*Anthoxanthum odoratum*)	*Rosa eglanteria* L. (*Rosa rubiginosa*)
Barbarea vulgaris Ait. f. (*Barbarea vulgaris*)	*Rumex crispus* L. (*Rumex crispus*)
Brassica nigra (L.) W. D. Jakoch (*Sinapis nigra*)	*Rumex obtusifolia* L. [*Rumex. obtusifolius* (sic)]
Cannabis sativa L. (*Cannabis sativa*)	*Salix alba* L. (*Salix alba*)
Chelidonium majus L. (*Chelidonium majus*)	*Salix vitellina* L. (*Salix vitellina*)
Cynoglossum officinale L. (*Cynoglossum officinale*)	*Scleranthus annuus* L. (*Scleranthus annuus*)
Daucus carota L. (*Daucus carota*)	*Stellaria media* L. (*Stellaria media*)
Datura stramonium L. (*Datura stramonium*)	*Taraxacum officinale* Weber (*Leontodon taraxacum*)
Holcus lanatus L. (*Holcus lanatus*)	*Trifolium pratense* L. (*Trifolium pratense*)
Leonurus cardiaca L. (*Leonurus cardiaca*)	*Trifolium repens* L. (*Trifolium repens*)
Marrubium vulgare L. (*Marrubium vulgare*)	*Verbascum blattaria* L. (*Verbascum blattaria*)
Nepeta cataria L. (*Nepeta cataria*)	*Verbascum thapsus* L. (*Verbascum thapsus*)
Pastinaca sativa L. (*Pastinaca sativa*)	*Veronica officinalis* L. (*Veronica officinalis*)
Phleum pratense L. (*Phleum pratense*)	

to Britain before being introduced in the United States.

The flurry of published floras that appeared after 1800 provides some of the best evidence we have of which deliberately introduced species were becoming naturalized. *Salix viminalis* L. ("*Salix viminalis*") (Pursh, 1814), *Crataegus monogyna* Jacq. ("*C. oxyacantha* L.") (Barton, 1818), *Acer negundo* L., *Salix babylonica* L., and *Salix alba* L. (Darlington, 1826) were all recognized as new members of the eastern U.S. flora. Sometimes the flora's author even knew the circumstances of a species' introduction. Darlington (1826) wryly attributed the establishment around West Chester, Pennsylvania, of *Leonurus marrubiastrum* L. to the gardening of Humphrey Marshall, a local horticultural enthusiast (Wilbert, 1908).

De Schweinitz (1832) assembled comprehensive information about deliberately introduced species that were becoming naturalized in the United States. His observations (de Schweinitz, 1832: 148) based on major categories of introduction are particularly informative: species "purposely brought hither to be cultivated, for the purposes of agriculture, or for some real or fancied value they possess" and others that had "been evidently involuntarily introduced with the imported seeds of agricultural plants. . . ." All 31 species that he listed as deliberate introductions (Table 2) remain naturalized in the United States, and a few have become invasive (e.g., *Poa pratensis* L., *Rumex crispus* L., *Verbascum thapsus* L.). Apparently, most of the current worst invaders in the United States had yet to arrive or were still undetected [e.g., *Bromus tectorum* L., *Lonicera japonica* Thunb., *Polygonum cuspidatum* Sieb. & Zucc., *Sorghum halepense* (L.) Pers.].

SEED CONTAMINANTS: EARLY IMMIGRANTS

In an era before herbicides and diligent seed sieving and inspection, seed lots of crop species varied radically in the extent to which they were contaminated with the seeds of extraneous and unwanted species. Some of the earliest records of nonindigenous plants in North America include species that likely arrived from Europe as seed contaminants, e.g., *Rumex acetosella* L. and *Rumex acetosa* L. (Cronon, 1983, and references therein). Many of these species have been intimately associated with crops through the strong selection provided by cultivation and post-harvest storage. Probably all seed-sown crops have their own array of seed mimics (Barrett, 1983); each mimic's phenology from germination to seed maturation is under selection by the cultivation cycle for its associated crop. Through this close synchrony between the life cycle of the crop and its mimics, cultivation applied to the crop could simultaneously benefit the mimics, leading to their naturalization (Mack, 2000).

We have only a sketchy list of species reputedly introduced as seed contaminants in the early settlement of the United States (Table 3). Given the general neglect of seed cleaning, there were, however, many possible immigrants among the ruderals and crop weeds of Europe. The native forage grasses in New England were deemed so unsuitable as forage that by the 1640s a market in European grass seed had already emerged around Narragan-

Table 3. Non-indigenous species in the United States considered by de Schweinitz (1832) to have arrived as seed contaminants among agricultural seeds. Some of the names employed by de Schweinitz are not in current nomenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Achillea millefolium L. (*Achillea millefolium*)	*Hypericum perforatum* L. (*Hypericum perforatum*)
Agrostemma githago L. (*Agrostemma githago*)	*Lamium amplexicaule* L. (*Lamium amplexicaule*)
Allium vineale L. (*Allium vineale*)	*Leucanthemum vulgare* Lam. (*Chrysanthemum leucanthemum*)
Anthemis cotula L. (*Anthemis cotula*)	*Linaria vulgaris* L. (*Antirrhinum linaria*)
Arctium lappa L. (*Arctium lappa*)	*Lithospermum arvense* L. (*Lithospermum arvense*)
Bromus secalinus L. (*Bromus secalinus*)	*Lolium perenne* L. (*Lolium perenne*)
Capsella bursa-pastoris (L.) Medik. (*Thlaspi bursa pastoris*)	*Plantago lanceolata* L. (*Plantago lanceolata*)
Cerastium fontanum Baumg. (*Cerastium vulgatum*)	*Poa annua* L. (*Poa annua*)
Cerastium glomeratum Thuill. (*Cerastium viscosum*)	*Polygonum aviculare* L. (*Polygonum aviculare*)
Cerastium semidecandrum L. (*Cerastium semidecandrum*)	*Raphanus raphanistrum* L. (*Raphanus raphanistrum*)
Chenopodium album L. (*Chenopodium album*)	*Setaria glauca* (L.) Beauv. (*Setaria glauca*)
Cirsium arevnse (L.) Scop. (*Carduus arvensis*)	*Sisymbrium officinale* (L.) Scop. (*Erysimum officinale*)
Cirsium vulgare (Savi) Ten. (*Cnicus lanceolatus*)	*Sonchus oleraceus* L. (*Sonchus oleraceus*)
*Commelina sativa**	*Urtica dioica* L. (*Urtica dioica*)
Elytrigia repens var. *repens* (L.) Desv. (*Triticum repens*)	*Urtica urens* L. (*Urtica urens*)
	Veronica agrestris L. (*Veronica agrestris*)
	Veronica arvensis L. (*Veronica arvensis*)

* Probably a corruption of *Camelina sativa* L. (Crantz.) (false flax).

sett Bay (Cronon, 1983, and references therein), providing ample opportunity for the importation of seed contaminants. Furthermore, Josselyn's (1672: 216) list, "Of such Plants as have sprung up since the English planted and kept Cattle in New England," includes non-indigenous species that are unlikely to have been introduced deliberately as pasture species but are often found as seed contaminants: "Shepard's purse" [*Capsella bursa-pastoris* (L.) Medik.], "Groundsel" [*Senecio vulgaris* L.], "Sow-thistle" [*Sonchus* sp.], "Cheek-weed" [*Stellaria media* (L.) Vill.]. Cronon (1983: 143) provided an account from 1652 in which settlers in the New Haven (Connecticut) colony were already debating without avail as to whether the ". . . spreading of sorrill [probably *Rumex crispus* L. or *Rumex acetosella* L.] in the corne fields . . ." could be stemmed. Kalm (1770) commented on European introductions that he saw along the North American eastern seaboard in 1748. Kalm (1770: 118) reported the informed opinion of John Bartram and other American botanists that "*Chenopodium album* [*Chenopodium album* L.] . . . is not a native of America, but has been brought over amongst other seeds from Europe." Kalm (1770: 119) also claimed that *Tanacetum vulgare* L., "which grows here and there in the hedges, on the roads, and near houses, was produced from European seeds." It likely arrived both through deliberate introduction (Mack, 1991) and as a seed contaminant.

Some early 19th century local and regional United States floras also cited species that reputedly arrived as seed contaminants. These statements reflect informed opinion, rather than documented cases. Nevertheless, they are among the very few accounts of these species in the United States that are nearly contemporaneous with their arrival. Barton (1818) described the flora in and around Philadelphia. He listed both *Lithospermum arvense* L. and *Lithospermum latifolium* Michx. as "introduced among grass seeds from Europe, but now naturalised." Pursh (1814) attempted to assemble a flora of the United States, although most of his own collections and exchanges originated in the eastern states from Virginia northward. He reported that *Anthoxanthum odoratum* L. ("*Anthoxanthum odoratum*"), *Festuca pratensis* Huds. ("*Festuca elatior*"), and *Centaurea cyanus* L. ("*Centaurea cyanus*") were either ". . . introduced with grass seeds from Europe" (Pursh, 1814: 65, 83) or "brought from Europe with the grain" (Pursh, 1814: 576).

De Schweinitz (1832: 151) provided the first specific attention to non-indigenous species arriving in the United States as seed contaminants. Although he did not provide explicit information as to how he determined which species were "introduced fortuitously with agricultural seeds," his list is nonetheless illuminating (Table 3). These species include many that remain today as crop seed contaminants or are ruderals, or both. All are now naturalized in the United States (Fernald, 1950). Some in his list also arrived through deliberate introduction, e.g., *Hypericum perforatum* L. (Haughton, 1978) and *Urtica dioica* L. (Uphof, 1968).

SEED CONTAMINANTS: A LONG-TERM MODE OF IMMIGRATION

The opportunity for non-indigenous species to arrive in the United States as seed contaminants grew throughout the 19th century, in part, because the United States remained surprisingly dependent on the routine importation of many crop seeds. Hicks (1895: 391) maintained that for an extraordinary list of crop and forage species, including, "alfalfa, beet, borage, broccoli, Brussels sprouts, cauliflower, chicory, cress, endive, kohl-rabi, radish, salsify, spinach, turnip, the seeds are grown abroad, as are also the seeds of many of our grasses, such as crested dog's tail, sheep fescue, meadow foxtail, perennial rye grass, and sweet vernal grass." In addition, "Of the following vegetables about one-half of the seeds are imported: Carrot, eggplant, leek, onion, parsley, parsnip, and pepper." Large fractions of the seeds needed for domestic production of cabbage, celery, chervil, kale, and lettuce were also imported (Hicks, 1895: 391).

Hicks (1895) and others (e.g., Ledoux, 1880; Ball, 1898) realized that such massive seed importation had created enormous opportunities for the inadvertent introduction of unwanted non-indigenous species. Furthermore, they recognized that a cultivated field, carefully tilled to enhance the crop, was equally advantageous for the emergence of extraneous species (Ledoux, 1880). Their concern had been heightened by recent events. An aggressive invader, *Salsola kali* L., had arrived in the 1880s as a contaminant in flax seed from Russia. By 1894 it had already invaded more than 90,000 km^2 in the wheat-producing regions in the Dakotas (Dewey, 1894). McCarthy (1888) contended that most of the weed flora in the United States was originally introduced and disseminated in the packages of imported seeds, an unsubstantiated claim but with some element of justification.

The problem was not, unfortunately, limited to inadequate seed-cleaning. Foreign seed merchants deliberately adulterated crop seeds with commercially worthless species: "charlock" (*Sinapis arvensis* L.) mixed with turnip and rutabaga seeds, "black medic" (*Medicago lupulina* L.) mixed with red clover, English rye mixed with the more valuable tall fescue and Italian rye (Hicks, 1895: 391). Ledoux (1880) reported that the seeds of ruderal species were routinely gathered in Austria and Bavaria for use as seed adulterants. In one 24.5 g sample of *Phleum pratense* L., Nobbe (1871) found 3329 extraneous seeds representing 31 taxa, including *Rumex acetosella* L., *Prunella vulgaris* L., *Cirsium arvense* (L.) Scop., *Sonchus asper* (L.) Hill ("*Sonchus asper* Villars"), and *Spergula arvense* L. In one extreme case, 90 percent of a Canadian seed lot sold in Michigan as clover consisted of extraneous and non-indigenous seeds. The unwanted seeds averaged 132,000 per kilo in this contaminated lot (Hicks, 1895: 393)—a large founder population that could readily benefit from any cultivation upon sowing. Some seed merchants in the United States were aware of this imported hazard. The Philadelphia seed firm I.V. Faust assured customers in its 1888 catalog that "We are most particular in the purchase of our grass seeds to procure them from a source where there is no danger of foreign seeds having become mixed with them, as we fully appreciate the great damage which some of these will create if once introduced upon the soil."

The response to foreign and domestic contamination was a flurry of state and federal legislation to examine commercial seeds, including seeds that had been directly imported from Europe (McCarthy, 1888; Hicks, 1895). Chester (1889) examined seed lots from domestic and foreign sources. Although it is difficult to distinguish between results for domestic and imported seed lots in his data, the litany of non-indigenous species he detected is consistent among all samples; naturalized species typically found in arable land and roadsides were being repeatedly introduced (Table 4). The diligence of the state-appointed seed analysts at the turn of the century led undoubtedly to curbing the introduction of unwanted non-indigenous species in the United States (Brown, 1941). Unfortunately, these regulatory practices were enacted long after many non-indigenous species had repeatedly entered the United States and become naturalized.

Despite the ample opportunity for non-indigenous species to arrive as seed contaminants before 1900, we detected few species for which there is a historic reference to their arrival in that mode: e.g., only 14 species within the central northeastern United States flora. This mode of introduction has nevertheless been significant. Some species not reported by any pre-1900 observer likely arrived in this manner and were simply overlooked. The United States probably derived many of the weeds of European arable fields simply through the frequency of their importation as seed contaminants. Furthermore, many species, such as *Amaranthus hybridus* L., *Anthemis cotula* L., *Capsella bursa-pastoris* (L.) Medik., *Chenopodium album*, *Nepeta cataria*, *Plantago major* L., and *Rumex acetosella* were continually being introduced and dispersed through the eastern United States by seed merchants (Table 4). Although these species had ar-

Table 4. Non-indigenous species detected repeatedly as seed contaminants in domestic and imported crop seeds in the late 19th century (Chester, 1889). Some of the names employed by Chester are not in current nonmenclatural usage, and he did not include scientific authorities for the species he listed. His names for these species appear parenthetically. The International Plant Names Index (http://www.ipni.org) was employed as the nomenclatural standard for plant names and authorities.

Agrostemma githago L. (*Agrostemma githago*)	*Nepeta cataria* L. (*Nepeta cataria*)
Amaranthus hybridus L. (*Amaranthus hybridus*)	*Plantago lanceolata* L. (*Plantago lanceolata*)
Anthemis arvensis L. (*Anthemis arvensis*)	*Plantago major* L. (*Plantago major*)
Capsella bursa-pastoris (L.) Medik. (*Capsella bursa-pastoris*)	*Polygonum* sp.
Carduus arvensis (L.) Scop. (*Cnicus arvensis*)	*Ranunculus* sp.
Chenopodium album L. (*Chenopodium album*)	*Rumex acetosella*
Echium vulgare L. (*Echium vulgare*)	*Rumex crispus* L. (*Rumex crispus*)
Hypericum perforatum L. (*Hypericum perforatum*)	*Setaria* sp.
Leucanthemum vulgare Lam. (*Chrysanthemum leucanthemum*)	*Stellaria media* L. (*Stellaria media*)
Lithospermum arvense L. (*Lithospermum arvense*)	*Verbascum thapsus* L. (*Verbascum thapsus*)

rived before 1800, the potential for an increase in their genetic variation in the United States would have continued long after these species' initial introduction, a function of the different European locales from which later-arriving populations were drawn (Novak & Mack, 2001).

SPECIES WITH UNKNOWN MODE OF IMMIGRATION TO THE UNITED STATES

We were unable to identify a pre-1900 use or other mode of introduction for approximately 30 percent of the species now naturalized in the regions we examined. Any assessment of the modes of introduction in naturalized floras is handicapped by the paucity and reliability of historic records. We avoided relying on common names to trace mode of introduction, unless a species' common name has been used consistently for several hundred years: e.g., henbane (*Hyoscyamus niger* L.), foxglove (*Digitalis purpurea* L.), shepherd's purse (*Capsella bursa-pastoris*). This criterion limited our ability to trace introductions before ca. 1780. Nevertheless, keen observers such as Josselyn (1672) and Kalm (1770) made invaluable observations.

Additional underestimate of deliberate introductions was likely because some species were introduced for unrecorded purposes. Their naturalized descendants are, however, a living link to a pre-1900 agrarian-based economy in the United States that relied on few imported commodities. Solutions to almost all material needs and desires were literally "home grown." Thus, *Hypericum perforatum* was used for medicinal purposes (Darlington, 1859) and as an object in religious services in 18th century Pennsylvania (Haughton, 1978). The dried heads of *Dipsacus fullonum* L. were used to comb wool (Fernald, 1950). If a plant was deemed valuable, its germplasm was imported, even if the likelihood of successful cultivation anywhere in the United States was low (Grieve, 1959; Stillé & Maisch, 1880). We may never discover all the purposes that our resourceful ancestors had for the range of species they so methodically imported.

Species introduced by all accidental (but undetected) modes occur in the Unknown Category, including those that can survive attached or within a vast array of cargo: hay, ballast, packing material, attached to livestock and clothing (Ridley, 1930; Mack, in press). But collectively they appear far less important than deliberate introduction as the mode by which plants have arrived in new ranges in the United States in the last 400 years (Mack, in press).

POST-1900 IMMIGRATION AND NATURALIZATION

Our emphasis has been on the link between pre-1900 plant introduction and subsequent cultivation and naturalization. Plant importation has continued, however, and new species continually become naturalized. Rejmanek and Randall (1994) reported that nine species had become naturalized in California between 1968 and 1993; deliberately introduced species are prominent in this list (*Catalpa bignonioides* Walt., *Nerium oleander* L., *Pinus pinea* L., *Pinus halepensis* Mill.). The post-1900 growth of the naturalized flora in the United States has likely been substantial. Henry and Scott (1981: 318) tallied the dates of introduction for the "alien component of the spontaneous Illinois vascular flora," species that apparently include all naturalized but also adventive species as well. They concluded that the woody and herbaceous component of this non-indigenous flora before 1922 was composed of 440 species; 163 species were added between 1922 and 1955, and another 208 non-indigenous species were added from 1956 to 1978. Many of these post-

Table 5. Tallies for the likely mode of entry (deliberate, accidental, deliberate & accidental, and unknown) for the naturalized angiosperm floras of South Australia, Hawaii, and Northern Europe. Numbers in each column except the last are percentages of the total naturalized flora surveyed. Sources for the modes of introduction are listed in the footnotes.

	Deliberate	Accidental	Deliberate & accidental	Unknown mode of introduction	Number of taxa
South Australia[1]	57	24	0	19	904
Hawaii[2]	57	39	0	4	813
Nordic continental countries[3, A]	36	44	13	<8	559
North Atlantic Islands[3, B]	16	61	9	14	46

[1] Kloot (1987).
[2] Wester (1992).
[3] Weidema (2000).
[A] Numbers are means of percentages for Norway, Sweden, Finland, and Denmark as derived from the data of Weidema (2000).
[B] Numbers are means of percentages for Greenland, Iceland, the Aland Islands, and the Faeroe Islands as derived from the data of Weidema (2000).

1900 plant immigrants to Illinois would have been deliberately introduced, including most, if not all, the woody immigrants (Reichard & Hamilton, 1997).

The proportions among deliberately and accidentally introduced 20th century immigrants that have become naturalized are better documented in Australia. Of the 290 weed, i.e., deleterious plant, incursions into Australia from 1971 to 1995 that have led to naturalizations, 65 percent of these species were introduced as ornamentals, and an additional 7 percent arrived as intended additions to agriculture (Groves, 1998). Thus, more than two-thirds of these species have had some degree of post-immigration cultivation. The proportion of species arriving in Australia through deliberate action continues a pattern set into motion centuries earlier among European colonies and their trading partners.

Detailed examination of the fate of introduced woody ornamental species across much of the 20th century in Canberra, Australia (Mulvaney, 2001), suggests an additional aspect of the importance of post-introduction cultivation. Mulvaney (2001) contended that the probability of a species becoming naturalized is a direct function of the number of recorded plantings of the species from 1909 through the mid 1980s. A similar explanation has been proposed to account for the naturalization of non-indigenous birds in New Zealand; persistence correlates with the intensity of the introduction efforts (Veltman et al., 1996). The more separate opportunities for non-indigenous species to be cultivated, the greater the probability some of its immigrants will be initially spared the full force of environmental stochasticity in the new range.

NATURALIZED SPECIES ARISE FROM DELIBERATE INTRODUCTIONS: A RECURRING PHENOMENON WORLDWIDE

Our chief goal was to evaluate in an objective manner the hypothesis that much of the U.S. naturalized flora has a historic link in its mode of entry to deliberate introduction and post-immigration cultivation. At the outset, we decided that our benchmark for rejecting this hypothesis would be the failure to detect that even half of the naturalized species had a history of pre-1900 use. Our hypothesis appears supported by our tallies (Table 1).

The plausibility of this link is further supported by evidence gathered among naturalized angiosperm floras worldwide. Wester (1992) examined the modes of introduction within the Hawaiian naturalized flora (Table 5). He concluded that the major mode of introduction had been deliberate (57%), and that a large fraction of these species had been introduced in ornamental horticulture. By coincidence, Kloot (1987) also found that at least 57 percent of the South Australia naturalized flora owed its arrival to deliberate transport (Table 5). Esler (1987) determined the modes of introduction (imported for use in either horticulture [including timber and shelter tree species] or agriculture [crop, pasture, and land reclamation], or accidental) for the 303 angiosperm species now naturalized in urban Auckland, New Zealand. Almost 93 percent of this naturalized flora was introduced deliberately, although the degree of post-immigration cultivation probably varies.

Recently, the mode of introduction has been assessed for non-indigenous species in Denmark, Finland, Iceland, Norway, and Sweden along with

the Åland Islands, the Faeroe Islands, and Greenland (Weidema, 2000). Here again, many naturalized species appear to have a history of deliberate introduction (e.g., *Inula helenium* L., *Lychnis chalcedonica* L., *Ornithogalum nutans* L., *Syringa vulgaris* L., *Spiraea salicifolia* L.), but the role of accidental introduction appears to be much larger than in the United States or South Australia. Among Nordic countries in continental Europe, about one-third of the naturalized species are considered to have been deliberately introduced, but more (44%) on average are believed to have been introduced accidentally as seed contaminants of cargo or carried by domesticated animals (Table 5).

These values from northern Europe require further interpretation. Among Nordic investigators there is apparently neither a consensus on the definition of "naturalized" (the values reported may also include adventive species for the floras of some countries) nor on an arrival date before which an immigrant species is deemed native (Weidema, 2000). Potentially more important is the much longer history of agriculture in northern Europe than farming by European colonists in the United States or South Australia. Several millennia of raising crops in northern Europe has given ample opportunity for species to have been introduced, both deliberately and inadvertently (Iversen, 1973). For some of these species, their mode of introduction is unknown [e.g., *Helleborus foetidus* L., *Potentilla micrantha* Ramond ex DC., *Digitalis lutea* L., *Silene tartarica* Pers.] (Weidema, 2000). Furthermore, some fraction of those species now considered native arrived so long ago with human settlement that any identification of erstwhile deliberate use is problematical. The much shorter histories of plant introductions into the "New Europes" in North America, Australia, and South America provide us with a sharper picture of the causes of plant naturalization than can be reconstructed from the records of plant dispersal by humans in Europe.

Needed now is experimentation that bridges the gap between two growing bodies of information: knowledge of the modes of plant introductions and naturalizations since A.D. 1500 (Kloot, 1987; Reichard & Hamilton, 1997; Groves, 1998; Mulvaney, 2001) and understanding of the stochastic forces to which immigrant populations are usually vulnerable (Menges, 1992, 1998; Mack, 1995, 2000). The design of experiments on the fate of immigrant populations (Panetta & Randall, 1994) could benefit from clues derived from the history of plant introductions. Experimental variables, including the sizes of the immigrant populations, the initial entry locales in the new range, and the character and extent of cultivation, could duplicate what is known about a species' early history in its new range. Once such investigations become widespread, our understanding of the causes of plant naturalization and subsequent invasion will likely become much clearer (Williamson, 1999; Williamson & Fitter, 1996).

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Appendix 1

Pre-1900 use of some of the naturalized angiosperm species that formed the tallies in Table 1 was indicated by their sale in these 19th century seed catalogs (Archives of the National Agricultural Library, Beltsville, Maryland).

Allen's annual catalogue of seeds. 1870. New York, New York.

Azell Bowditch. 1854. A descriptive catalogue of flower seeds for sale. Boston, Massachusetts.

Barr, G. H. and Co. 1853. Catalogue of agricultural and horticultural implements field and garden seeds and fertilizers.

J. Bartram and Son. 1807. A catalogue of trees, shrubs, and herbaceous plants, indigenous to the United States of America. Philadelphia, Pennsylvania.

B. K. Bliss and Sons. 1870. Catalogue of seeds. Springfield, Massachusetts.

Charles H. B. Breck. 1842. Catalogue of vegetable, herb, tree, flower, and grass seeds, for sale at the New Seed store. Boston, Massachusetts.

Robert Carr. 1828. Bartram's catalogue of trees, shrubs, and herbaceous plants, indigenous to the United States of America. Philadelphia, Pennsylvania.

Bernard M'Mahon. 1804. A catalogue of American seeds, & c. Philadelphia, Pennsylvania.

Bernard M'Mahon. s. d. A catalogue of garden, herbs, flowers, tree, shrub and grass seeds. Philadelphia, Pennsylvania.

Pomeroy and Marshall. 1857. (no title). Mobile, Alabama.

Warren's Garden and Nurseries. 1845. Annual descriptive catalogue of fruit and ornamental trees. Boston, Massachusetts.

Messrs. Winship. 1833. Annual catalog of the fruit and ornamental trees and plants, cultivated for sale at the Brighton Nurseries by Messrs. Winship. Boston, Massachusetts.

Winter and Co. 1841. Catalogue of fruit and ornamental trees. [Linnean Botanic Garden and nursery (late of the messrs. Princes).] Flushing, New York.

Winter and Co. 1844–1845. Catalogue of fruit and ornamental trees. [Linnean Botanic Garden and nursery (late of the messrs. Princes).] Flushing, New York.

THE DODO WENT EXTINCT (AND OTHER ECOLOGICAL MYTHS)

Stuart L. Pimm[1]

Abstract

The scientific consensus is that human impacts are driving species to extinction hundreds to thousands of times faster than expected from the natural background rate. Critics challenge this. Perhaps giving them more credit than they deserve, I examine four concerns. First, that the extinction crisis is not real. It is and high rates of extinction are the rule, not the exception, within well-known taxa. The second criticism dismisses the problem as one restricted just to islands. It is not. Island species have special vulnerabilities, but they are far more locally abundant within their ranges than are continental species with the same range size. There are large numbers of locally rare, continental species with small geographic ranges that are threatened by human impacts. A third criticism notes the few species that became extinct following the clearing of forests from eastern North America in the 19th century, casting doubt upon the relationship between habitat loss and species loss. Analysis of this case history shows that exactly as many species of birds were lost as expected, for the region had very few species to lose. Extensions to species-rich areas such as Southeast Asia and the Atlantic coast of Brazil confirm the expected calibrations with an interesting caveat. Forest losses predict the number of threatened species—those on the verge of extinction—not the number of extinctions. This leads to the final criticism: that there have been too few recent extinctions. The reply is that in these regions the deforestation is more recent and species do not go extinct immediately. Some doomed species can linger for decades—as did the now-extinct species in eastern North America.

Key words: deforestation, extinction, species-area curves.

Among scientists there is a broad consensus that species are going extinct in unusual numbers. I will not assemble the evidence for this directly because there are recent reviews (May et al., 1995; Pimm, 2001; Pimm et al., 1995). Rather, I wish to tackle the critics who dispute this consensus. Whatever one thinks of them and those who finance some of them, however one scorns their willingness to ignore volumes of inconvenient facts, the critics persist. They will likely continue to do so while individuals gain financially from short-term environmental destruction. Over the last decade, I have listened to these critics and, perhaps giving them more credit than they deserve, assembled the science to rebut them directly. The synthesis I present here is one based largely on my own work on birds. This is not because it is unique—far from it; there is an abundance of evidence to counter these critics. Rather, it is an attempt to lay out cohesive, linked arguments into a recipe that readers can readily apply to other taxa.

There are four criticisms.

1. The extinction crisis is not real. Rather, it is a "doomsday myth" (Budiansky, 1993). It is the "facts, not the species" that are endangered (Simon & Wildavsky, 1993: A23), the estimates of extinction rates are "strident, inconsistent, and data-free" (Mann & Plummer, 1995). Since the humid tropical forests of the Amazon, Congo and New Guinea, and elsewhere hold the majority of species, their fate is closely tied to the fate of species. Stott (1999) had this to say about them: "'Tropical rain forest' does not exist and never has existed."

2. Those who accept that unusual numbers of extinctions have occurred can still proceed to dismiss their significance. "The dodo went extinct" proclaims the *Oxford English Dictionary.* Most recent extinctions, like the dodo, have been on islands. The implication is that island species are wimpy, naïve, and unsophisticated. Perhaps island species had it coming to them and the urbane, sophisticated species that populate continents may not share their fate.

3. Habitat destruction does not cause extinctions—look at eastern North America, Budiansky (1993) urged. Projections of future high extinction rates such as those by Wilson (1988) and Raven (1988) combine well-documented rates of tropical forest destruction and a model to predict species loss from habitat loss. How good are those predictions? Eastern North America was cleared of its deciduous forests from 1750 to 1900, yet suffered few known extinctions. Critics argue that we simply do not know how to predict the numbers of

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species that will be lost as tropical forests disappear.

4. In what is mostly a rehashing of earlier myths, Lomborg (2001) seemed to be asking where are the bodies to prove an extinction crisis? Some early efforts did indeed suggest that there should be lots of extinct species by now. For example, "one seventh to one fifth of all species" extinct within what would now have been the last two decades (Barney, 1980: 328). There are not nearly enough, though to continue the metaphor, there are the requisite number of seriously wounded ones. So are these species really dying off at the expected rate—or are our concerns about them misplaced?

I consider each of these myths in turn.

1. The Extinction Crisis Is Not Real

Has humanity increased extinction rates beyond the background rates expected without our impacts? Those who argue that we have not are claiming that far too few species have gone extinct in the recent past. Where should we look for the extinct species that would reject this assertion?

Pacific islands are the obvious place to start, for they were the planet's last habitable areas to be colonized. Polynesians reached them only within the last 1000 to 4000 years. The evidence of human impact is freshest here. (The evidence of human-caused mass extinctions in Australia, Madagascar, and the Americas grows more compelling each year, however (Flannery, 1999)). Pacific island birds provide unambiguous evidence of massive extinction (Pimm et al., 1994; Steadman, 1995). The bones of many bird species persist into, but not through, archaeological zones showing human presence.

I will consider the Hawaiian islands in detail. We know 43 bird species only from their bones. Yet bird bones are fragile and easily destroyed. We may never find bones of all the now-extinct species, so how many are missing? The bone record would be complete only if all the recent species—those collected or seen in the last two centuries—were also found as bones. The proportion of recent species *also* found as bones estimates how complete the sample of species found *only* as bones is. The proportion is about a half: across the Hawaiian islands, we estimate there are about 40 species missing from the record (Pimm et al., 1994). Add this number to the 43 known species extinctions and the body count rises to 83.

James Cook found the Hawaiian islands in 1778. International trade and colonization followed within a generation. These new people cleared forests and introduced cattle and goats. These destroyed native plants as unprepared for large mammalian herbivores as the birds were for the rats and pigs the Polynesians brought with them on their earlier colonization. Today, our only records of 18 species of birds are the specimens collected by 19th century naturalists. The body count rises to 101.

What remains in the Hawaiian islands today? Pimm et al. (1994) recorded that a dozen species are so rare that there is little hope of saving them. If we cannot find these species, then they probably cannot find each other. A further dozen we can find, but in numbers so small that their future survival is uncertain. Of an estimated 136 species, only 11 survive in numbers that suggest a confident future.

Similar extinctions followed across the Pacific. Over the roughly 1000 years, as the Polynesians colonized the Pacific from New Zealand, north to Hawai'i, and east to Easter Island, they exterminated ~1000 species of birds or ~10% of the world total (Pimm et al., 1994; Curnutt & Pimm, 2001). On some islands, they exterminated all the bird species they encountered.

They extensively cleared lowland forests, especially the drier ones (and used only Stone-Age technology to do so). Birds were not the only victims of these colonizations, incidentally. Of 980 native Hawaiian plants, 84 are extinct and 133 have wild populations of fewer than 100 individuals (Sohmer, 1994). These plant extinctions were the consequence of recent human colonizations. Quite how many plant species the Polynesians exterminated we may never know.

Few species groups leave traces; land snails are one and their losses illustrate the bizarre but extensive devastation that human actions can effect. A predatory snail, *Euglandina rosea*, introduced to many Pacific islands to control another introduced snail, *Achatina fulica*, ate to extinction hundreds of taxa of native *Achatinella* and *Partula* land snails (Hadfield, 1986; WCMC, 1992). (I use the term "taxa" to include recognized geographically distinct populations. Taxonomic uncertainties often raise and sink their specific status. For those that are now extinct we may never resolve the issue.)

Nor are Pacific islands unusual in their species losses. As European explorers moved from their coastal waters from the early 1500s, Mauritius, Rodrigues, and Réunion in the Indian Ocean lost 33 species of birds, including the dodo, 30 species of land snails, and 11 reptiles. St. Helena and Madeira in the Atlantic Ocean have lost 36 species of land snails (WCMC, 1992).

These examples raises two obvious questions. The first is whether their numbers are unusual or,

alternatively, how many species should we expect to go extinct each year? The background, that is, pre-human rates of extinctions fluctuate considerably over time and surely vary from one species group to the next. However, a convenient (and likely conservative) background rate of extinction is about "one in a million" (May et al., 1995; Pimm et al., 1995). Only about one in a million species should terminate their existence naturally within a year. The bird extinction rate is closer to one bird species per year from a sample pool of only 10,000 bird species. This means that bird extinctions are running 100 times the expected rate.

The second obvious question: Do we find evidence of massive extinctions *only* on islands?

2. The Dodo Went Extinct (Too Bad!)

If island species were the only ones at risk, then we consider their loss to be unfortunate, but relax in the confidence that they were especially vulnerable. This argument fails at two levels. The first failure is that high rates of extinctions occur in places other than islands. Here are three examples:

(1) A distinct and unusual flora defines the Cape Floristic Region, which occupies a small area of the southern tip of Africa. It comprises several vegetational types of which the fynbos is dominant in area and contributes the most species. Of the Region's 9030 species (Goldblatt & Manning, 2002 this issue), 36 species have become extinct in the last century, and some 618 species are *threatened* (Cowling, 1992). (I will always use "threatened" in a specific, technical sense to mean those species thought likely to become extinct within at most a few decades. Quite how long threatened species are likely to last is a topic I discuss later.)

(2) In North America's rivers, Williams et al. (1992) described the mussels and clams in the Mississippi and St. Lawrence river basins. Of the 297 North American taxa of the two families Unionidae and Margeritifidae, an estimated 21 have likely gone extinct since the end of the last century. Another 120 taxa are threatened. Miller et al. (1989) found that of ~950 taxa of freshwater fish in the United States, Canada, and Mexico, 40 have become extinct in the last 100 years. Northern lakes, southern streams, wetlands, and desert springs are very different habitats, yet all have lost species.

(3) Of the 60 species of recent mammal extinctions worldwide, 19 are from Caribbean islands (WCMC, 1992). This repeats the pattern of high extinction rates of islands, and I will not consider them further. Interestingly, 18 more were in Australia (WCMC, 1992), representing ~6% of its non-marine mammal species. The extinctions have been equally divided between the southern arid zone—a sparsely inhabited area of mostly spinifex desert and extensive pastoralism—and the wheat belt of the southern tip of Western Australia—where 95% of the natural woodland has been cleared (Short & Smith, 1994). Another 43 Australian mammal species have been lost from more than half of their former ranges or survive on protected offshore islands (Burbidge & McKenzie, 1989).

These examples refute the criticism that extinctions are restricted to islands. In reviewing these and other examples I am struck by the diversity of taxa and ecosystems they encompass. Across these examples, indeed for all well-known taxa, recent extinction rates are 100 to 1000 times the expected rate (Pimm et al., 1995; Lawton & May, 1995).

The second failure of the "it's just islands" criticism is more surprising. Certainly, greater numbers and greater fractions of recent species extinctions have been on islands than on continents. For instance, since 1600, 97 of the total 108 bird extinctions have been on islands (Collar et al., 1994). Island biotas are uniquely vulnerable to the human introduction of previously absent herbivores, predators, diseases, and other natural enemies (Pimm, 1991). Species on continents are not so ecologically naïve.

There is another major factor that determines threat. Most threatened species have small geographic ranges (Stattersfield et al., 1998) and island species' ranges are inevitably smaller than continental ones. For a given range size, how do the island and continental fractions of threatened species compare?

Manne et al. (1999) calculated the ranges of all the passerine birds in the Americas and their associated islands. (They comprise roughly a quarter of all bird species.) To separate the effects of range size, and island versus continental distribution, we calculated the breeding range—henceforth, just "range." Some of the continental species inhabit montane habitat "islands" isolated by a "sea" of lowland habitats. We ask whether these montane species suffer different levels of threat and so separate them from lowland species.

Manne et al. showed that for the 14 lowland, 8 montane, and 27 island species with ranges smaller than 1000 km^2 the proportions of threatened species are high, but uncertain because of the small sample sizes. Despite these uncertainties, for these small ranges there is no evidence that island species are more vulnerable than those on continents. Perhaps one should expect this. Tiny ranges should

make species vulnerable to habitat loss, hunting, and other threats wherever the species live.

Their most surprising conclusion emerges for range sizes between 1000 km² and 100,000 km². Much *smaller* fractions of montane and island species are threatened than of lowland species. At ranges larger than 100,000 km² the proportions are uniformly small in all three groups.

This unexpected result at intermediate ranges has several possible explanations, but we consider that local abundance is the most likely (Manne & Pimm, 2001). We find that island species with a range of (say) 10,000 km² are often locally abundant on their island. Montane species with small ranges are also locally numerous within their ranges. These examples of numerous species with small ranges have no match in continental lowlands. There, species with such small ranges are almost always very rare within those ranges (Brown, 1984; Gaston et al., 1997). A reasonable explanation for the abundance of island species is competitive release (MacArthur et al., 1972). With fewer competitors, island species are able to attain higher densities and are thus less likely to be threatened.

In sum, corrected for range size, continental species are more—not less—likely to be threatened. This unexpected vulnerability of continental species offsets their putative ecological sophistication and experience of predators and other threats. There seems to be no reason why continental species will be spared the high rates of extinction humanity first vested on insular species.

3. Trash the Rainforests Just as Americans Did their Forests: Nothing Will Happen

Extensive reductions in the forests of eastern North America occurred during the 19th century. Surprisingly, only four bird species went extinct: passenger pigeon, Carolina parakeet, ivory-billed woodpecker, and Bachman's warbler from reasons wholly or mostly from habitat loss. Birds are well-known, so we cannot plead ignorance of their extinctions. Critics use this apparent discrepancy to claim that fears about massive global extinctions based on habitat losses are "simply wrong" (Budiansky, 1994). Just how many species *should* have gone extinct as a consequence of the loss of forests?

The answer comes from an extension of one of the most well calibrated ecological relationships (Rosenzweig, 1995). The function, $S = cA^z$, frequently provides a good description of the relationship between the size of an area, A, and the number of species, S, that it contains; c and z are constants. For real islands surrounded by sea, z is usually about ¼ (Rosenzweig, 1995).

Now, suppose we extend this to forest "islands" that remain amid a "sea" of deforestation. We can then predict the reduction in numbers of species from $S_{original}$ to S_{now} as the habitat's area is reduced from $A_{original}$—the original extent of forest—to A_{now}—the area that now remains as forest "islands." The proportion of species lost ($S_{now}/S_{original}$) should be $(A_{now}/A_{original})^z$. Thus S_{now} equals $S_{original}(A_{now}/A_{original})^z$ and the number of extinctions, $S_{extinct}$ equals $S_{original} - S_{now}$. Notice that we need an estimate of the value of z, but not of c. Does this recipe work or are one or more of its assumptions flawed?

In North America, some 48% of the area covered by the eastern forest at the time of European settlement (1620) was still wooded at the point of its lowest forest cover (roughly 1872: Pimm & Askins, 1995). With $A_{1872}/A_{1620} = 0.48$ and $z = 0.25$, we predict that ~17% of the region's 160 forest birds (27 species) should have become extinct. It is this prediction, some six times greater than the four well-documented extinctions, that causes controversy.

Does this discrepancy cast doubt on the predictions of species losses from habitat reduction? It does not. Those who point to the small number of observed extinctions in the eastern forests mean *global extinctions*—species that are lost everywhere. The prediction of 27 extinctions is based on the number of species lost only within the region. Some of these 160 bird species would survive even if *all* the eastern forests were cleared. Their distributions across the boreal forests of Canada or into Central America would afford them a refuge while U.S. forests were cleared.

How many species *could* become globally extinct if all the eastern forests were felled? Which species are found *only* in these forests, that is, how many species are endemic to them? The answer is only 28. Now 17% of 28 ≈ 4.76. This prediction is roughly three-quarters of a species higher than the number of extinctions observed. I will not push my luck to argue that the endangered red-cockaded woodpecker, *Picoides borealis*, is three-quarters of its way to extinction. The observed and predicted numbers are remarkably close. This case history is not the counterexample critics claim it to be. North America lost few species because it had relatively few species to lose.

What happens in areas of the world that stand to lose many species? My colleagues and I have applied this recipe to two such areas. The first is insular Southeast Asia (Brooks et al., 1997, 1999a). The region comprises four archipelagos: the Phil-

ippines, the Greater Sundas (Java, Sumatra, and Borneo), northern Wallacea (Sulawesi and the Moluccas), and the Lesser Sundas. Their forests hold 585 endemic species of bird—roughly 20 times that of America's eastern forest, in half the area. About 10% of the original area is cleared per decade. Most of this deforestation has occurred recently and ~60% of the original area is still forested. Unlike the previous example, deforestation has not yet caused any confirmed bird extinctions in insular Southeast Asia. Extinctions take time following habitat loss, a point to which I must return.

What does the species-area recipe predict about the details of where extinctions will eventually occur? Across the region, some areas still have most of their forests: Borneo had ~67%, for example, when we assembled the forest cover data. (Forests are shrinking rapidly, however.) Other areas have almost none: Cebu, in the Philippines has < 1%. And some areas have more endemic species than others. Using the recipe, we predicted the numbers of threatened bird and mammal species in each of these four archipelagos, island by island. With a few, interesting exceptions, there is a statistically striking correspondence between the numbers of species we predict should go extinct and those that are currently threatened. Borneo, for example, has 38 endemics of which only 3 are considered to be threatened: the recipe predicts 4. Sulawesi and associated islands also have about two-thirds of their forest remaining, but there are 146 endemic species strewn across these islands. The recipe predicts 14 should be threatened with extinction and 16 actually are. In contrast, in the Philippines, the islands of Mindoro and the western and central Visayas have 19 endemic species; all are threatened, while the recipe only predicts that 10 should be. Where the recipe fails it usually does so by underestimating the number of threatened species: when little forest remains, other factors—including hunting and invasive species—add to the threats.

The second area is the Atlantic coast forest of Brazil (Brooks & Balmford, 1996). It has 214 endemic bird species. The area has four major subdivisions and for each there is a close match between the numbers of threatened species and those we predict should become extinct solely on the basis of habitat loss. (The lowland forests are particularly hard hit, with only 2% of the forest remaining; the recipe predicts that 7 of 11 endemic species should be threatened; 9 are threatened.)

In sum, we have a well-calibrated ecological relationship that predicts how many species should become extinct following the loss of habitat across three continents. Given enough time for the species to die, as in North America, the predictions are supported. Worldwide, for every extinct species of bird there are 10 that are threatened. We predict these much larger numbers, too, from the loss of habitat in endemic-rich parts of South America and tropical Asia. But we are still left with the criticism that the species have not yet expired. There is a lingering uncertainty that perhaps our worst fears will not be realized. That leads to the final criticism.

4. Where Are the Bodies?

If we are in the midst of an extinction crisis, why are more species not going extinct? The reply is that it takes time for (metaphorically) fatally wounded species to expire. The point is made by the extinctions of birds in eastern North America. The low point of forest cover for these forests was about 1870; the four fatally wounded birds lingered for several decades, perhaps even a century, before finally expiring.

This "many decades" matches many other sources of information. It fits with the IUCN definition of "threatened"—a widely held expert opinion that threatened species will likely go extinct within a few decades. And it fits exactly with the few studies that have explicitly examined forest fragments and watched how fast species disappear from them (Brooks et al., 1999b; Pimm & Brooks, 2000). These studies suggest a species survivorship curve with a half-life of roughly 50 years. That is, half the species that will eventually expire do so within the first 50 years, half of what remain expire in the next 50 years, and so on. Given these results, over what time period might the pending massive loss of species from human actions unfold?

Pimm and Raven (2000) provided several answers. The first comes from considering the large fraction of species living within tropical forests and how fast those forests are shrinking. A second answer comes from looking at the hotspots—such places as the Atlantic coast forests of Brazil and Southeast Asia where endemic species are particularly concentrated.

About two-thirds of all species occur in the tropics, most of them in tropical humid forests (Raven, 1980). Such forests include both evergreen rainforests and more seasonal ones. They originally covered from 14 to 18 million km^2, depending on the exact definition, and about half the original area remains (Skole & Tucker, 1993). Much of the forest reduction is recent, and clearing now eliminates about 1 million km^2 of tropical forest in 5–10 years. Burning and selective logging severely damages

several times the area that is cleared (Nepstead et al., 1999; Cochrane et al., 1999).

To convert habitat loss to species loss, one extends the species-area relationship derived for islands to predict how many species will not survive in habitat fragment "islands" that remain amid a "sea" of converted land—as described above. Then one updates the numbers each year as the total forested area shrinks. Species that are classified as threatened will expire in decades to come and they will be joined by other species for which we are only now destroying their habitats. The doomed species do not all die at once, but are spread over time as determined by the species survivorship curve. Combining these results gives an extinction curve that I view as no more than a first sketch that captures a few salient features.

Because the species-area curve is non-linear, the clearing to date of half the humid forests should have fatally wounded 15% of their species. This is the case. Some 12% of all plants are threatened (Walter & Gillett, 1998). This estimate is likely to be an underestimate since many rare species have yet to be described. Of course, clearing the remaining half of these forests would eliminate the other 85% of their species. Thus, the numbers of fatally wounded species should accelerate rapidly to a peak by mid century. They will be joined by ever-larger fractions of species jeopardized by the interaction between the assumed constant rate of forest clearing and the non-linear species-area curve.

The relative height of the peak depends critically on the fraction of habitat that remains. A value of 5% would protect about 50% of all the forests' species. Smaller percentages of remaining forest would lead to very much smaller estimates of surviving species. (About 5% of the world's land surface is protected at present, but that percentage includes disproportionately large areas of desert and tundra ecosystems. Protecting 5% of tropical forests will require a considerable effort.)

The time delays before extinction mean that there will be far fewer species going extinct at present than are being fatally wounded. The model predicts that current extinction rates should be modest—on the order of a hundred species per year, per million species. This matches current estimates (Pimm et al., 1995). There are as many bodies as we expect, not far fewer. Extinction numbers will also peak in mid century, but will be spread out over a century or more thereafter.

Modest tinkering with parameters does not alter the "fewer extinctions now, many more later" feature of this curve, but the contribution of Myers et al. (2000) does. They show that roughly 30 to 50% of plant, amphibian, reptile, mammal, and bird species occur in 25 hotspots that individually are no more than 2% of the ice-free land surface. These diverse taxa demonstrate that species with small ranges are numerous and they are extraordinarily concentrated. Nature has put her terrestrial species in relatively few baskets. The sample applies to the oceans: fishes and other organisms dependent on coral reefs are similarly concentrated (McAllister et al., 1994).

Myers et al. (2000) showed that human impacts are malevolent, not random. Across the 25 hotspots, an average of 12% of the original primary vegetation remains. This percentage should be compared to the roughly 50% for tropical forests as a whole. Even within the hotspots, Myers et al. found that the areas richest in endemic plant species have proportionately the least remaining vegetation and the smallest areas currently protected (Fig. 1).

A second way to sketch the unfolding extinction assumes that conservation actions immediately protect all the remaining habitat areas within the hotspots. Applying the species-area curve to the individual hotspots predicts that 18% of all their species would eventually go extinct. [Since Myers et al. (2000) showed that hotspots hold 30–50% of all species, see above, this percentage is also consistent with the fraction of currently threatened species.] Yet another sketch assumes that the hotspots' higher than global average rate of habitat loss continues for another decade until only the areas currently protected remain. The hotspots would eventually lose 44% of all their species (Pimm & Raven, 2000).

None of these three sketches captures the inadequacy of some of the protected areas, the so-called "paper parks." Nor do these ideas consider the added threat of global warming that will doubtless limit the effectiveness of sharply delimited, small reserves. Also excluded are the major threats that invasive species—introduced and weedy species—pose to the remaining species. Often listed as the most important factor in causing threat and extinction, the impacts of invasive species on islands are well known. Continents are vulnerable, too. Plant introductions are a major threat to the Cape Region of South Africa, for instance (Cowling, 1992).

The distinction between these three sketches is artificial. Many species live in tropical forests that are also hotspots. Yet others live in tropical forests that are not and some live in hotspots that are not tropical forests. Nonetheless, the sketches capture views of the size and time-scale of the processes driving the unfolding extinction.

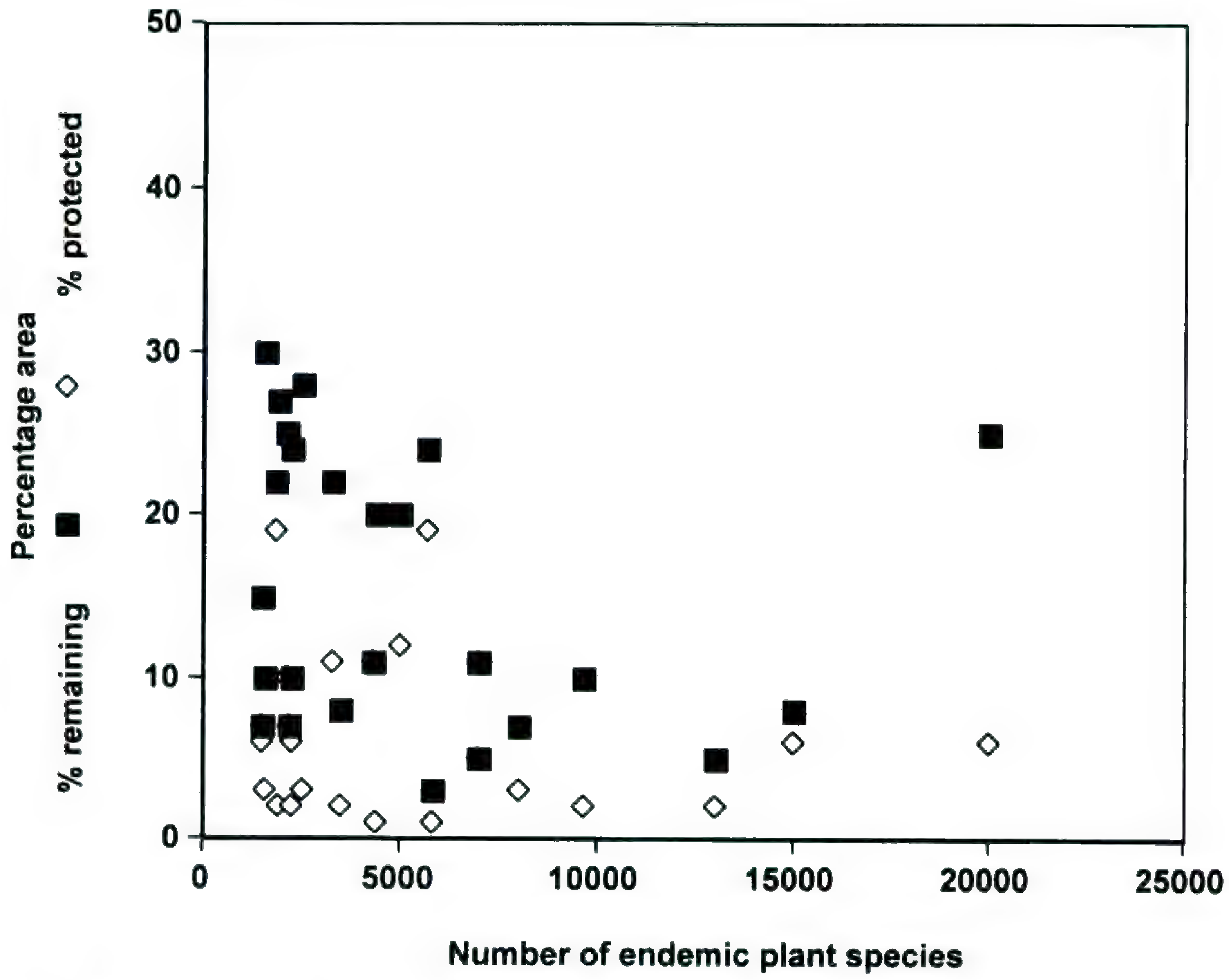

Figure 1. The percentage of the original habitat remaining and the percentage of the original habitat protected are generally smaller in those hotspots that contain the greatest number of endemic plant species. From data in Myers et al. (2000).

The first process is the rapidly accelerating loss of presently extensive, but rapidly shrinking, tropical forests. Protecting substantial and representative areas requires prompt action. This is unlikely to happen unless industrialized nations become more deeply involved with funding conservation in developing ones. Without such action, the loss of species from these areas will overtake the loss of species from hotspots within a few decades.

The second process is the rate of loss of species from hotspots. Losses here should dominate for the next few decades, since hotspots are already severely fragmented. [By definition: Myers et al. (2000) defined hotspots to have unusual numbers of endemic species and to have suffered disproportionate habitat losses.] Only immediate conservation actions, including restoration of damaged habitats, can prevent further species loss. And unless there is immediate action to salvage the remaining unprotected areas, the species losses will more than double. As Myers et al. pointed out, the current unprotected areas constitute only a little more than 1 million km^2. High concentrations of small-ranged species make many species vulnerable, but equally they permit a concerted effort to prevent future extinctions.

Conclusions

The dodo did not go extinct. Humanity bludgeoned it into oblivion. With it went 10% of the planet's birds and, in all probability, similar fractions of other poorly known species of plants and animals. That we did not identify and name all the species that disappeared is not a credible argument for their continued survival. The Vietnam memorial on the Mall in Washington, D.C., is a poignant list of all the Americans who died in the U.S.A.'s war in that country. A far smaller list of names appears on a memorial in the village in England where I was born to men who died in France between 1914 to 1918. I recognize those names as just a sample and, relative to the village's small population, readily extrapolate to the massive slaughter of men across the entire country. While a complete list of extinct species would be useful, it is not essential to perceive or to estimate the size of the current crisis.

Dismissing the threats of future extinctions from the few that have occurred in North America is likewise the consequence of misinterpretation. Most of the recent known bird extinctions on continents happened in North America following European

colonization. Quite what happened in Europe when its forests were cleared centuries earlier we may never know. Consequently, North America is the crucial case history of forest and species loss. It teaches that we lost 4 of 28 of its endemic forest bird species, almost exactly what the species-to-area calibrations predict on the basis of a 50% reduction of forests. (Three more species were hunted to extinction: the great auk, the Labrador duck, and the Eskimo curlew.) The major tropical forests in the Amazon, the Congo, and New Guinea have already lost half their area, are shrinking by the day, and yet they hold more than 10 times the number of bird species that were found in eastern North America. The hotspots are already depleted even further. The North American case history is most telling when scaled appropriately.

Some scientists have overestimated the numbers of species that should be going extinct per year at present. The fault lies solely with the assumption that species would die out immediately. Some do, but most manage to linger. We have yet to realize the 10% loss of species—roughly the fraction of well-known species that are threatened—because the destruction of the most species-rich ecosystems has only unfolded in the last half century. Yet this overestimation is simply fixed by changing the text from predictions of "actual extinctions" to predictions of species "being on an inexorable path to extinction." Unless we protect more of the planet's remaining natural areas, by the end of this century that distinction will seem absurdly trivial.

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THE GLOBAL 200: PRIORITY ECOREGIONS FOR GLOBAL CONSERVATION[1]

David M. Olson[2,3] *and Eric Dinerstein*[2]

Abstract

A global strategy to conserve biodiversity must aim to protect representative examples of all of the world's ecosystems, as well as those areas that contain exceptional concentrations of species and endemics. Although lacking the richness of tropical forests, deserts, tropical lakes, and subpolar seas all contain distinct species, communities, and ecological phenomena. We analyzed global patterns of biodiversity to identify a set of the Earth's terrestrial, freshwater, and marine ecoregions that harbor exceptional biodiversity and are representative of its ecosystems. We placed each of the Earth's ecoregions within a system of 30 biomes and biogeographic realms to facilitate a representation analysis. Biodiversity features were compared among ecoregions to assess their irreplaceability or distinctiveness. These features included species richness, endemic species, unusual higher taxa, unusual ecological or evolutionary phenomena, and the global rarity of habitats. This process yielded 238 ecoregions—the Global 200—comprised of 142 terrestrial, 53 freshwater, and 43 marine priority ecoregions. Effective conservation in this set of ecoregions would help conserve the most outstanding and representative habitats for biodiversity on this planet.

Key words: biodiversity, conservation, ecoregions, endemism, global, phenomena, priority-setting, representation.

Tropical rain forests rightfully receive much conservation attention as they may contain half of the world's species. A comprehensive strategy for conserving global biodiversity, however, must strive to save the other 50 percent of species and the distinctive ecosystems that support them. For example, while they may not support the rich communities seen in tropical rain forests or coral reefs, tropical dry forests, tundra, polar seas, and mangroves all harbor unique species, communities, adaptations, and phenomena. Some of these biomes, such as tropical dry forests and Mediterranean-climate shrublands, are more threatened than are tropical rain forests and require immediate conservation action. To lose examples of these assemblages would represent an enormous loss of global biodiversity.

Limited funding compels the conservation community to be strategic and earmark the greatest amount of resources to protect the most outstanding and representative areas for biodiversity. On a global scale, this requires identifying large regions with exceptional levels of species richness or endemism, or those with unusual ecological or evolutionary phenomena. We must also target representative examples of all of the world's biomes within each biogeographic realm where they occur (Fig. 1). Because of distinct biogeographic histories, similar kinds of ecosystems found on different continents or in different ocean basins support unique assemblages of species and higher taxa. For this reason, global strategies should strive to conserve examples of every biome in each realm where it occurs for terrestrial, freshwater, and marine biodiversity (Olson & Dinerstein, 1998; Udvardy, 1975; Dasmann, 1974). Here we present the Global 200—an attempt to identify a set of ecoregions whose conservation would achieve this goal of saving a broad diversity of the Earth's ecosystems (Figs. 2, 3). This paper expands and updates an earlier analysis by Olson and Dinerstein (1998). Several additional ecoregions have been identified through ongoing regional analyses (e.g., Wikramanayake et al., 2001) and the marine Global 200 have been reduced, largely due to combining several adjacent areas

[1] We thank the regional experts, biologists, and conservationists who contributed their time and knowledge to the conservation analyses that went into the Global 200. J. Leape and C. Hails have provided critical support for this effort. The staff of WWF contributed greatly to the regional assessments from which the map is derived. We thank World Wildlife Fund's Conservation Science Program for their contribution to the analysis and preparation of the Global 200, specifically R. Abell, T. Allnutt, C. Carpenter, J. D'Amico, P. Hurley, K. Kassem, H. Strand, M. Taye, M. Thieme, W. Wettengel, E. Underwood, E. Wikramanayake, I. Itoua, C. Loucks, T. Ricketts, S. Walters, P. Hedao, M. McKnight, Y. Kura, J. Morrison, and G. Powell. J. Martin-Jones and U. Lagler helped in many ways to facilitate the completion of this project. We thank the staff of the WWF Network, including all of the national organizations, various field offices and programs, and associates, for their review and comments on earlier drafts.

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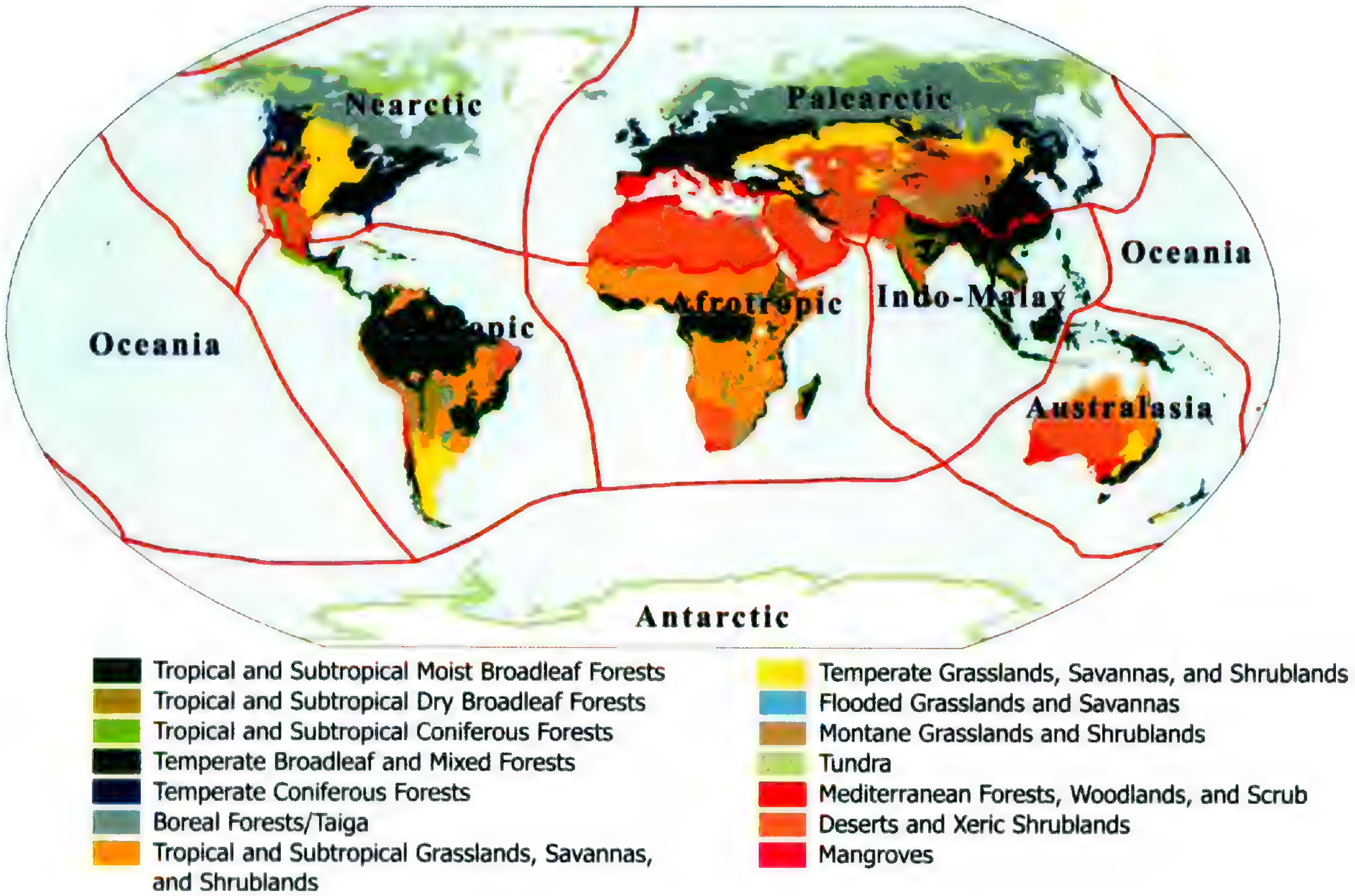

Figure 1. Terrestrial biomes, terrestrial and freshwater biogeographic realms, and marine biogeographic realms (sensu Dasmann, 1974; Udvardy, 1975).

into larger units. In addition, the conservation status of all ecoregions has been estimated.

Ecoregions are regional-scale (continental-scale) units of biodiversity. We define ecoregions as a relatively large area of land or water containing a characteristic set of natural communities that share a large majority of their species, ecological dynamics, and environmental conditions (Dinerstein et al., 1995; Groves et al., 2000). They function effectively as coarse-scale conservation units because they encompass similar biological communities, and their extent roughly coincides with the area over which key ecological processes interact most strongly (Orians, 1993).

For each of the Earth's 30 terrestrial, freshwater, and marine biomes (formerly referred to as major habitat types in our previous analysis), we compared the biodiversity of each constituent ecoregion. Those ecoregions whose levels of biodiversity were considered exceptional (that is, highly distinctive or irreplaceable; see Dinerstein et al., 1995; Pressey et al., 1994) for their biome, or which were considered the best example of a biome within a realm (even if none of the candidates harbored exceptional biodiversity), were identified as areas of particular importance for achieving global conservation goals. This prioritization yielded 238 ecoregions—the Global 200—comprised of 142 terrestrial, 53 freshwater, and 43 marine ecoregions nested within 30 biomes and 8 terrestrial and freshwater biogeographic realms and 13 marine biogeographic subdivisions (Table 1).

Delineation of Ecoregions

Terrestrial Ecoregions

Dasmann (1974) and Udvardy (1975) were the first to conduct a global representation analysis for terrestrial conservation. Dasmann's system of 198 biotic provinces and Udvardy's 193 units are nested within 7 biogeographic realms and 13 terrestrial biomes and 1 freshwater biome. Both these geographic models serve as logical frameworks for analyses of global representation.

The relative coarseness of Dasmann's and Udvardy's biotic provinces, however, limits their utility as regional conservation planning tools as many distinctive biotas may remain unrecognized. We believed a more finely resolved map of biodiversity patterns was required, one that mapped distinctive biotas within single, continuous biomes. This called for intensive regional analyses of biodiversity patterns across five continents by synthesizing existing

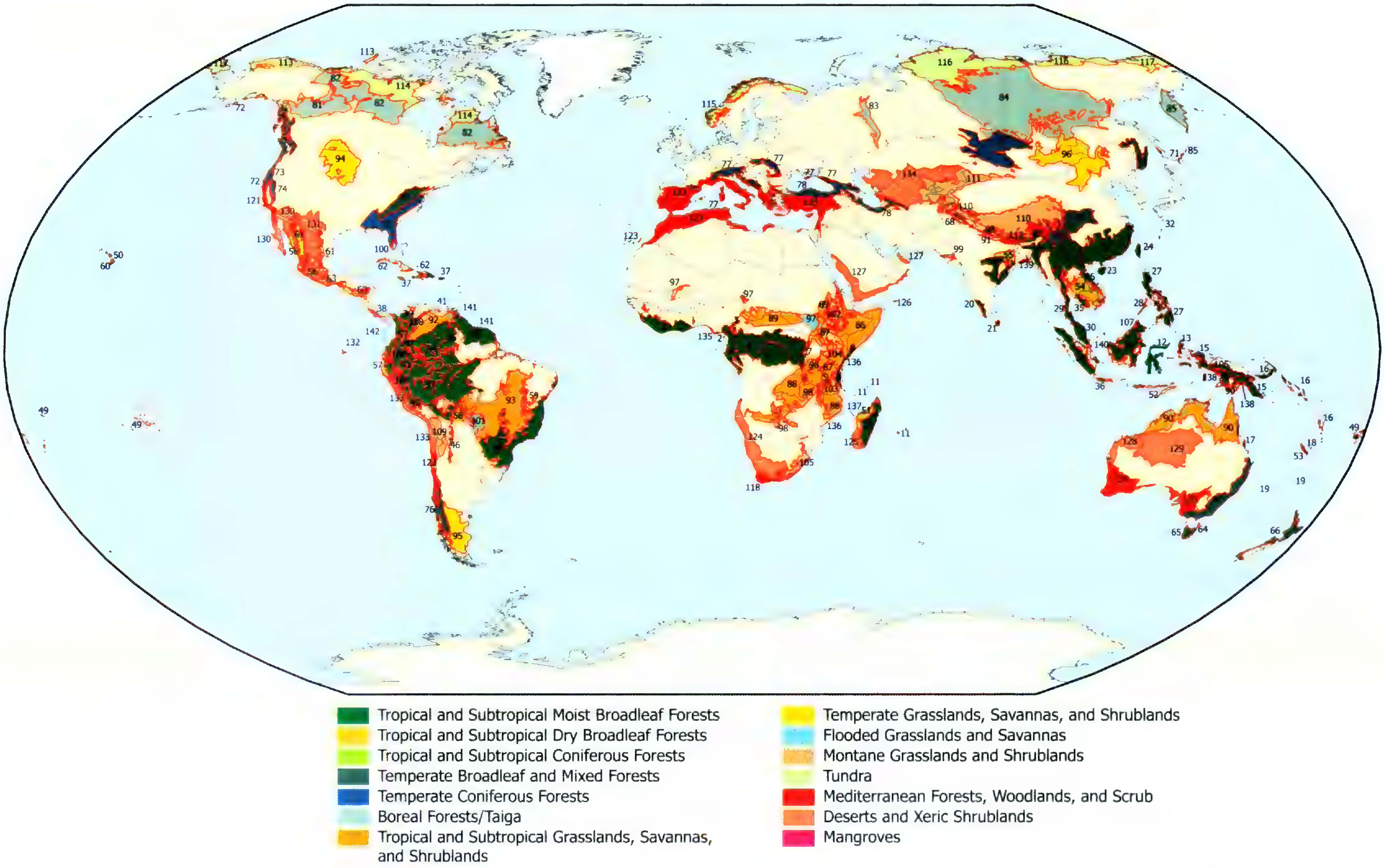

Figure 2. The terrestrial Global 200 ecoregions targets ecoregions with outstanding biodiversity features and representative value. The numbers correspond to the ecoregions listed in Table 1.

Table 1. Global 200 ecoregions organized by biomes and biogeographic realms. the estimated conservation status for each ecoregion is noted as follows: CE for critical or endangered, V for vulnerable, and RS for relatively stable or intact. Ecoregions marked by asterisks (*) represent new areas presently under review for elevation to Global 200 status based on their biodiversity features and representation value.

TERRESTRIAL REALM	
TROPICAL AND SUBTROPICAL MOIST BROADLEAF FORESTS	
Afrotropical	
1. Guinean Moist Forest	CE
2. Congolian Coastal Forests	CE
3. Cameroon Highland Forests	CE
4. Northeastern Congo Basin Moist Forests	V
5. Central Congo Basin Moist Forests	RS
6. Western Congo Basin Moist Forests	V
7. Albertine Rift Montane Forests	CE
8. East African Coastal Forests	CE
9. Eastern Arc Montane Forests	CE
10. Madagascar Forests and Shrublands	CE
11. Seychelle and Mascarene Moist Forests	CE
Australasian	
12. Sulawesi Moist Forests	CE
13. Moluccas Moist Forests	V
14. Southern New Guinea Lowland Forests	V
15. New Guinea Montane Forests	RS
16. Solomons-Vanuatu-Bismarck Moist Forests	V
17. Queensland Tropical Forests	V
18. New Caledonia Moist Forests	CE
19. Lord Howe–Norfolk Islands Forests	CE
Indo-Malayan	
20. Southwestern Ghats Moist Forests	CE
21. Sri Lankan Moist Forests	CE
22. Northern Indochina Subtropical Moist Forests	V
23. Southeast China-Hainan Moist Forests	CE
24. Taiwan Montane Forests	V
25. Annamite Range Moist Forests	V
26. Sumatran Islands Lowland and Montane Forests	CE
27. Philippine Moist Forests	CE
28. Palawan Moist Forests	CE
29. Kayah-Karen/Tenasserim Moist Forests	V
30. Peninsular Malaysian Lowland and Montane Forests	V
31. Borneo Lowland and Montane Forests	CE
32. Nansei Shoto Archipelago Forests	CE
33. Eastern Deccan Plateau Moist Forests	CE
34. Naga-Manupuri–Chin Hills Moist Forests	V
35. Cardamom Mountains Moist Forests	RS
36. Western Java Montane Forests	CE
Neotropical	
37. Greater Antillean Moist Forests	CE
* (Lesser Antillean Moist Forests)	CE
38. Talamancan-Isthmian Pacific Forests	RS
39. Chocó–Darién Moist Forests	RS
40. Northern Andean Montane Forests	CE
41. Coastal Venezuela Montane Forests	V
42. Guianan Moist Forests	RS
43. Napo Moist Forests	V
44. Rio Negro-Juruá Moist Forests	CE
45. Guayanan Highland Moist Forests	RS

Table 1. Continued.

46. Central Andean Yungas	CE
47. Southwestern Amazonian Moist Forests	RS
48. Atlantic Forests	CE
Oceania	
49. South Pacific Island Forests	CE
50. Hawaii Moist Forests	CE
TROPICAL AND SUBTROPICAL DRY BROADLEAF FORESTS	
Afrotropical	
51. Madagascar Dry Forests	CE
Australasia	
52. Nusa Tenggara Dry Forests	CE
53. New Caledonia Dry Forests	CE
Indo-Malayan	
54. Indochina Dry Forests	CE
55. Chhota-Nagpur Dry Forests	CE
Neotropical	
56. Mexican dry Forests	CE
57. Tumbesian-Andean Valleys Dry Forests	CE
58. Chiquitano Dry Forests	CE
59. Atlantic Dry Forests	CE
Oceania	
60. Hawaii Dry Forests	CE
TROPICAL AND SUBTROPICAL CONIFEROUS FORESTS	
Nearctic	
61. Sierra Madre Oriental and Occidental Pine-Oak Forests	CE
Neotropical	
62. Greater Antillean Pine Forests	CE
63. Mesoamerican Pine-Oak Forests	CE
TEMPERATE BROADLEAF AND MIXED FORESTS	
Australasia	
64. Eastern Australia Temperate Forests	CE
65. Tasmanian Temperate Rain Forests	V
66. New Zealand Temperate Forests	V
Indo-Malayan	
67. Eastern Himalayan Broadleaf and Conifer Forests	V
68. Western Himalayan Temperate Forests	CE
Nearctic	
69. Appalachian and Mixed Mesophytic Forests	V
Palearctic	
70. Southwest China Temperate Forests	V
71. Russian Far East Temperate Forests	V
TEMPERATE CONIFEROUS FORESTS	
Nearctic	
72. Pacific Temperate Rainforests	CE
73. Klamath-Siskiyou Coniferous Forests	CE
74. Sierra Nevada Coniferous Forests	CE
75. Southeastern Coniferous and Broadleaf Forests	CE
Neotropical	
76. Valdivian Temperate Rainforests/Juan Fernández Islands	CE
* (Juan Fernández Islands and Desventuradas Islands)	CE
Palearctic	
77. European-Mediterranean Montane Mixed Forests	CE

Table 1. Continued.

78. Caucasus-Anatolian-Hyrcanian Temperate Forests	CE
79. Altai-Sayan Montane Forests	V
80. Hengduan Shan Coniferous Forests	RS
BOREAL FORESTS/TAIGA	
Nearctic	
81. Muskwa/Slave Lake Boreal Forests	RS
82. Canadian Boreal Forests	RS
Palearctic	
83. Ural Mountains Taiga	V
84. Eastern Siberian Taiga	RS
85. Kamchatka Taiga and Grasslands	RS
TROPICAL AND SUBTROPICAL GRASSLANDS, SAVANNAS, AND SHRUBLANDS	
Afrotropical	
86. Horn of Africa Acacia Savannas	V
87. East African Acacia Savannas	V
88. Central and Eastern Miombo Woodlands	V
89. Sudanian Savannas	CE
Australasia	
90. Northern Australia and Trans-Fly Savannas	RS
Indo-Malayan	
91. Terai-Duar Savannas and Grasslands	CE
Neotropical	
92. Llanos Savannas	V
93. Cerrado Woodlands and Savannas	V
TEMPERATE GRASSLANDS, SAVANNAS, AND SHRUBLANDS	
Nearctic	
94. Northern Prairie	CE
* Tallgrass prairies	
Neotropical	
95. Patagonian Steppe	CE
Palearctic	
96. Daurian Steppe	V
FLOODED GRASSLANDS AND SAVANNAS	
Afrotropical	
97. Sudd-Sahelian Flooded Grasslands and Savannas	CE
98. Zambezian Flooded Savannas	V
Indo-Malayan	
99. Rann of Kutch Flooded Grasslands	CE
Neotropical	
100. Everglades Flooded Grassland	V
101. Pantanal Flooded Savannas	CE
MONTANE GRASSLANDS AND SHRUBLANDS	
Afrotropical	
102. Ethiopian Highlands	CE
103. Southern Rift Montane Woodlands	CE
104. East African Moorlands	RS
105. Drakensberg Montane Shrublands and Woodlands	CE
Australasia	
106. Central Range Subalpine Grasslands	RS
Indo-Malayan	
107. Kinabalu Montane Shrublands	RS
Neotropical	
108. Northern Andean Paramo	RS
109. Central Andean Dry Puna	V
Paleartic	
110. Tibetan Plateau Steppe	V

Table 1. Continued.

111. Middle Asian Montane Steppe and Woodlands	V
112. Eastern Himalayan Alpine Meadows	RS
TUNDRA	
Nearctic	
113. Alaskan North Slope Coastal Tundra	RS
114. Canadian Low Arctic Tundra	RS
Palearctic	
115. Fenno-Scandia Alpine Tundra and Taiga	V
116. Taimyr and Siberian Coastal Tundra	RS
117. Chukote Coastal Tundra	RS
MEDITERRANEAN FORESTS, WOODLANDS, AND SCRUB	
Afrotropical	
118. Fynbos	CE
Australasia	
119. Southwestern Australia Forests and Scrub	CE
120. Southern Australia Mallee and Woodlands	CE
Nearctic	
121. California Chaparral and Woodlands	CE
Neotropical	
122. Chilean Matorral	CE
Palearctic	
123. Mediterranean Forests, Woodlands, and Scrub	CE
DESERTS AND XERIC SHRUBLANDS	
Afrotropical	
124. Namib-Karoo-Kaokoveld Deserts	V
125. Madagascar Spiny Thicket	CE
126. Socotra Island Desert	CE
127. Arabian Highland Woodlands and Shrublands	V
Australasia	
128. Carnavon Xeric Scrub	CE
129. Great Sandy-Tanami Deserts	RS
Nearctic	
130. Sonoran-Baja Deserts	RS
131. Chihuahuan-Tehuacán Deserts	V
Neotropical	
132. Galápagos Islands Scrub	V
133. Atacama-Sechura Deserts	V
Palearctic	
134. Central Asian Deserts	CE
MANGROVES	
Afrotropical Atlantic	
135. Gulf of Guinea Mangroves	CE
Afrotropical Indian	
136. East African Mangroves	CE
137. Madagascar Mangroves	CE
Australasia	
138. New Guinea Mangroves	RS
Indo-Malayan Indo-Pacific	
139. Sundarbans Mangroves	CE
140. Greater Sundas Mangroves	CE
Neotropical Atlantic	
141. Guianan–Amazon Mangroves	RS
Neotropical Pacific	
142. Panama Bight Mangroves	RS

Table 1. Continued.

Freshwater Realm	
LARGE RIVERS	
Afrotropical	
143. Congo River and Flooded Forests	RS
Indo-Malayan	
144. Mekong River	V
Nearctic	
145. Colorado River	CE
146. Lower Mississippi River	CE
Neotropical	
147. Amazon River and Flooded Forests	RS
148. Orinoco River and Flooded Forests	RS
Palearctic	
149. Yangtze River and Lakes	CE
LARGE RIVER HEADWATERS	
Afrotropical	
150. Congo Basin Piedmont Rivers and Streams	RS
Nearctic	
151. Mississippi Piedmont Rivers and Streams	CE
Neotropical	
152. Upper Amazon Rivers and Streams	RS
153. Upper Paraná Rivers and Streams	CE
154. Brazilian Shield Amazonian Rivers and Streams	V
LARGE RIVER DELTAS	
Afrotropical	
155. Niger River Delta	CE
Indo-Malayan	
156. Indus River Delta	CE
Palearctic	
157. Volga River Delta	CE
158. Mesopotamian Delta and Marshes	CE
159. Danube River Delta	CE
160. Lena River Delta	RS
SMALL RIVERS	
Afrotropical	
161. Upper Guinea Rivers and Streams	CE
162. Madagascar Freshwater	CE
163. Gulf of Guinea Rivers and Streams	V
164. Cape Rivers and Streams	CE
Australasia	
165. New Guinea Rivers and Streams	RS
166. New Caledonia Rivers and Streams	CE
167. Kimberley Rivers and Streams	RS
168. Southwest Australia Rivers and Streams	CE
169. Eastern Australia Rivers and Streams	CE
* (New Zealand Rivers and Streams)	V
Indo-Malayan	
170. Xi Jiang Rivers and Streams	CE
171. Western Ghats Rivers and Streams	CE
172. Southwestern Sri Lanka Rivers and Streams	V
173. Salween River	V
174. Sundaland Rivers and Swamps	V
Nearctic	
175. Southeastern Rivers and Streams	CE
176. Pacific Coastal Rivers and Streams	CE
177. Gulf of Alaska Coastal Rivers and Streams	RS
Neotropical	
178. Guianan Freshwater	RS
179. Greater Antillean Freshwater	CE
* (Southern Cone Freshwater, especially Valdivian region)	V
* (Atlantic Coast rivers of SE Brazil, Uruguay)	V
Palearctic	
180. Balkan Rivers and Streams	CE
* (expansion to Mediterranean region in general including western North Africa)	
181. Russian Far East Rivers and Wetlands	RS
* (Aral Sea Basin, particularly Syr- and Amu-Dar'ya Rivers)	CE
LARGE LAKES	
Afrotropical	
182. Rift Valley Lakes	CE
Neotropical	
183. High Andean Lakes	CE
Palearctic	
184. Lake Baikal	V
185. Lake Biwa	CE
SMALL LAKES	
Afrotropical	
186. Cameroon Crater Lakes	CE
Australasia	
187. Lakes Kutubu and Sentani	RS
188. Central Sulawesi Lakes	V
Indo-Malayan	
189. Philippines Freshwater	CE
190. Lake Inle	V
191. Yunnan Lakes and Streams	CE
Neotropical	
192. Mexican Highland Lakes	CE
XERIC BASINS	
Australasia	
193. Central Australian Freshwater	V
Nearctic	
194. Chihuahuan Freshwater	CE
Palearctic	
195. Anatolian Freshwater	CE
Marine Realm	
POLAR	
Antarctic	
196. Antarctic Peninsula and Weddell Sea	RS
Arctic	
197. Bering Sea	V
198. Barents-Kara Seas	CE
TEMPERATE SHELF AND SEAS	
Mediterranean	
199. Mediterranean Sea	CE
North Temperate Atlantic	
200. Northeast Atlantic Shelf Marine	CE
201. Grand Banks	CE
202. Chesapeake Bay	V
North Temperate Indo-Pacific	
203. Yellow Sea	CE
204. Okhotsk Sea	RS

Table 1. Continued.

Southern Ocean	
205. Patagonian Southwest Atlantic	V
206. Southern Australian Marine	RS
207. New Zealand Marine	V
TEMPERATE UPWELLING	
North Temperate Indo-Pacific	
208. California Current	RS
South Temperate Atlantic	
209. Benguela Current	V
South Temperate Indo-Pacific	
210. Humboldt Current	V
211. Agulhas Current	RS
TROPICAL UPWELLING	
Central Indo-Pacific	
212. Western Australia Marine	RS
Eastern Indo-Pacific	
213. Panama Bight	V
214. Gulf of California	CE
215. Galápagos Marine	V
Eastern Tropical Atlantic	
216. Canary Current	CE
TROPICAL CORAL	
Central Indo-Pacific	
217. Nansei Shoto	CE
218. Sulu-Sulawesi Seas	CE
219. Bismarck-Solomon Seas	RS
220. Banda-Flores Sea	V
221. New Caledonia Barrier Reef	RS
222. Great Barrier Reef	RS
223. Lord Howe–Norfolk Islands Marine	RS
224. Palau Marine	V
225. Andaman Sea	V
Eastern Indo-Pacific	
226. Societies/Marquesas/Tuamotus Marine	V
227. Hawaiian Marine	V
228. Rapa Nui Marine	RS
229. Fiji Barrier Reef & Marine	RS
Western Indo-Pacific	
230. Maldives, Chagos, Lakshadweep Atolls	V
231. Red Sea	V
232. Arabian Sea	CE
233. East African Marine	V
234. West Madagascar Marine	V
* (The Mascarene Islands are under consideration due to high numbers of endemic reef fish)	
* (The Maldives are under consideration for extension to include Sri Lanka and southern Indian coast)	
Western Tropical Atlantic	
235. Mesoamerican Reef	CE
236. Greater Antillean Marine	CE
237. Southern Caribbean Sea	V
238. Northeast Brazil Shelf Marine	V

classifications from finer scales.[4] Furthermore, delineations were conducted in collaboration with hundreds of regional experts and included extensive literature reviews. The result is a digital map of 867 terrestrial ecoregions, classified within biomes and realms, to be used for priority-setting analyses (Olson et al., 2001). This map provides a much more detailed picture of how species assemblages are distributed across the world. The increased resolution is most apparent in the tropics where Dasmann (1974) and Udvardy (1975) identified 115 and 117 provinces respectively, compared to 463 terrestrial ecoregions.

Dasmann and Udvardy both went on to assess how well existing protected areas represented the Earth's terrestrial biomes and realms. Biotic provinces with little or no protection were identified as priorities. The Global 200 analysis frames the goal of prioritization differently: We ask which regions should be a priority for conservation action (e.g., designating and strengthening protected areas) because of their outstanding biodiversity features or their representation value. We also apply this question to the terrestrial, freshwater, and marine realms.

FRESHWATER ECOREGIONS

Separate analyses of freshwater and terrestrial ecoregions were conducted because the distribution of freshwater biodiversity diverges from terrestrial patterns. Freshwater ecoregions were based on several regional analyses and consultations with regional experts.[5] Currently, the Global 200 analysis effectively targets the majority of freshwater priorities. Some targets, however, may change as we near completion of a global map of freshwater ecoregions that is based on a standard level of biogeographic resolution and relevant biomes.

[4] Victor (1955), Freitag (1971), Zohary (1973), Miyawaki (1975), Yim (1977), Chinese Vegetation Map Compilation Committee (1979), Wiken (1986), New Zealand Department of Conservation (1987), Noirfalise (1987), Changchun Institute of Geography and Chinese Academy of Sciences (1990), Kurnaev (1990), Bohn (1994), Krever et al. (1994), Dinerstein et al. (1995), Ecological Stratification Working Group (1995), Gallant et al. (1995), Hilbig (1995), Omernik (1995), Thackway & Cresswell (1995), Mongolian Ministry for Nature and the Environment et al. (1996), European Topic Centre on Nature Conservation (2000), Ricketts et al. (1999), WWF/IUCN (1994, 1995, 1997), Bohn & Katenina (1996), Wikramanayake et al. (2001), S. Gon (pers. comm.).

[5] Hocutt & Wiley (1986), Frest & Johannes (1991), WCMC (1992), Maxwell et al. (1995), Oberdorff et al. (1995), Kottelat & Whitten (1996), Olson et al. (1999), Abell et al. (2000), Thieme et al. (in press).

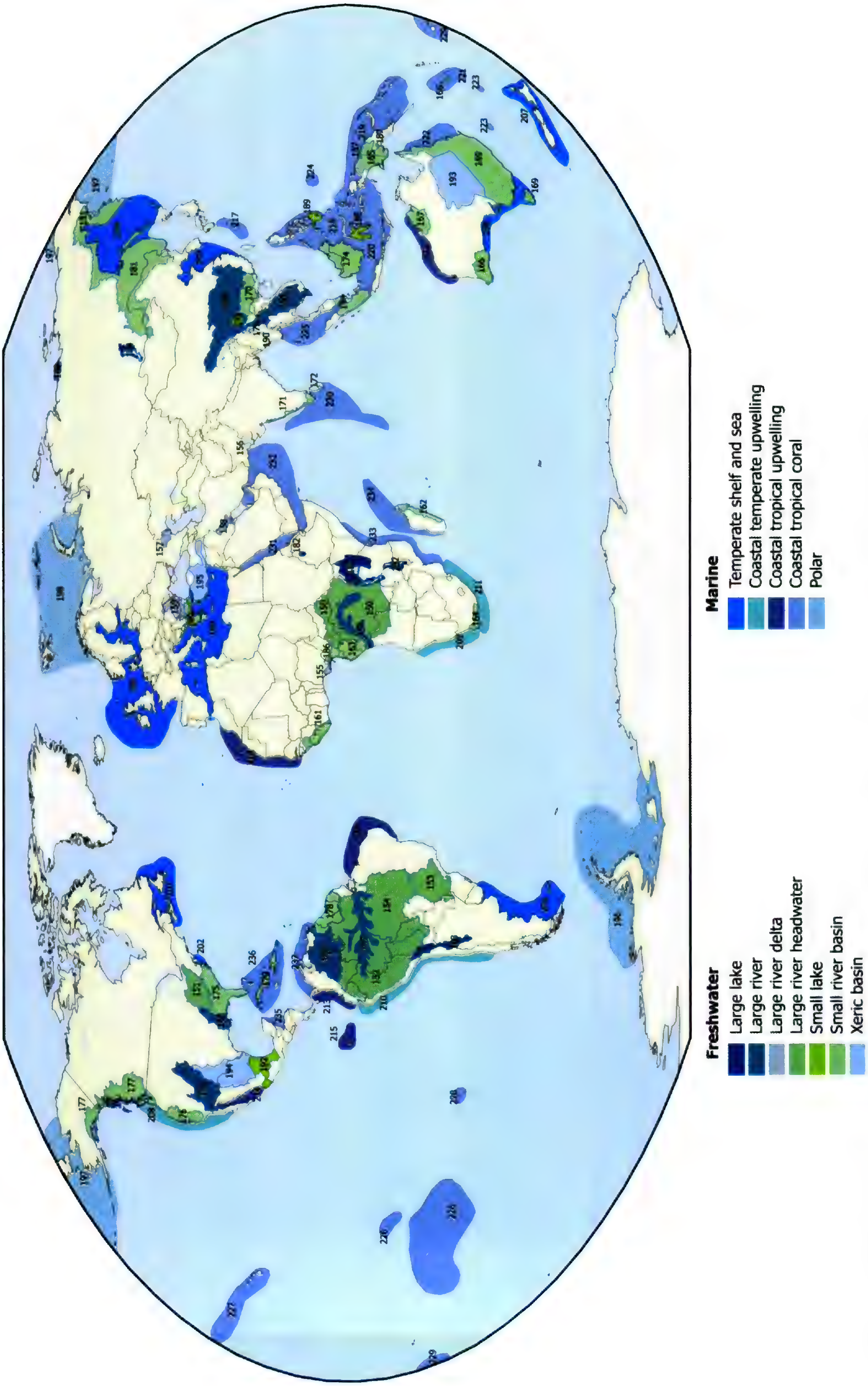

Figure 3. The freshwater and marine Global 200 ecoregions. The numbers correspond to the ecoregions listed in Table 1.

MARINE ECOREGIONS

Relative to most terrestrial and freshwater ecoregions, marine ecological and biogeographic units are more spatially and temporally dynamic (Sherman et al., 1990) and therefore more challenging to delineate. Marine ecoregions delineated by the Global 200 are derived from a synthesis of global and regional spatial schemas, review of the available literature[6] and consultations with experts. Kelleher et al. (1995), Sherman et al. (1990), Longhurst (1998), and Bailey (1998) served as the primary sources for the Global 200. Our base map does not cover deep water ecosystems (i.e., pelagic, abyssal, or hadal) nor are its biogeographic units as finely resolved as the maps used in the freshwater or terrestrial analyses. We believe that several forthcoming and detailed analyses of marine biodiversity around the world (Callum Roberts, pers. comm. 2001, Gerald Allen, pers. comm. 2002) will be useful in testing and improving the accuracy of our results. As in the land-based analyses, the delineation of marine ecoregions is intended to highlight general regions within which characteristic animals, plants, ecological interactions, and biophysical processes occur.

BIOGEOGRAPHIC RESOLUTION

The majority of Global 200 regions are composed of an aggregation of continental-scale ecoregions. This reflects the coarser level of biogeographic resolution applied on a global scale. For example, whereas 12 terrestrial units were delineated for the island of New Guinea in the regional analysis (Wikramanayake et al., 2001), only 5 Global 200 units are recognized. The ecoregions that were combined are adjacent, related by habitat type, and are biogeographically similar at a global scale. Appoximately a third of the ecoregions used in the regional analyses correspond directly to Global 200 ecoregions. The specific location and configuration of boundaries of Global 200 ecoregions do not present exact target areas for detailed planning. Rather, Global 200 ecoregions are primarily intended to spotlight regions of exceptional importance for strategic decision-making.

SELECTION CRITERIA FOR THE GLOBAL 200

Selection of the Global 200 draws heavily from the results of intensive regional analyses of biodiversity conducted over the last several years (Krever et al., 1994; Dinerstein et al., 1995; Olson et al., 1999; Ricketts et al., 1999; Abell et al., 2000; Wikramanayake et al., 2001; Burgess et al., in press; Thieme et al., in press). Within each biome and biogeographic realm, the relative importance of ecoregions was classified at one of four levels: globally outstanding, regionally outstanding (e.g., Neotropics, Atlantic Ocean), bioregionally outstanding (e.g., Caribbean), or locally important. The criteria used to prioritize ecoregions for the Global 200 are the same as those used for the regional assessments. We chose the set of ecoregions within each biome that were considered to harbor biodiversity that was globally outstanding or regionally outstanding based on the parameters described below.

These parameters were weighted and measured in the regional analyses as illustrated in Appendix 1. The weight assigned to the different parameters varied by biome to better address specific patterns of biodiversity and ecological dynamics.

SPECIES RICHNESS AND ENDEMISM

Richness values were first corrected for area. We then divided the range of values for the set of ecoregions sharing the same biome and realm into four categories based on natural breaks. Globally outstanding ecoregions were compared with those identified for other realms to ensure consistency. In general, widely recognized global and regional centers of richness and endemism were selected for Global 200 status. The precision of the data varied considerably as illustrated by richness and endemism values for vascular plants in temperate conifer and tundra biomes (Tables 2, 3).

HIGHER TAXONOMIC UNIQUENESS

The presence of an endemic higher taxon (genus or family) would contribute more to an ecoregion's biotic distinctiveness than would an endemic species. Some ecoregions are notable for biotas that contain unique taxa at higher taxonomic levels than species (Vane-Wright et al., 1991; Williams et al., 1991; Gaston & Williams, 1993; Forey et al., 1994; Williams & Humphries, 1994). For example, the moist forests of northeastern Australia, northern New Zealand, and New Caledonia are recognized as having a number of the most primitive lineages of conifers and flowering plants in the world (WWF/IUCN, 1994–1997).

UNIQUE ECOLOGICAL OR EVOLUTIONARY PHENOMENA

Some ecoregions were elevated to Global 200 status because of their extraordinary ecological

[6] Hayden et al. (1984), IUCN (1988), Sherman (1990), Croom et al. (1992), Ray & Hayden (1993), Kelleher et al. (1995), Groombridge & Jenkins (1996), Ormond et al. (1997), Sullivan & Bustamante (1996), Longhurst (1998).

Table 2. Estimated richness and endemism (expressed as number of species) of native vascular plant species for temperate coniferous forest ecoregions around the world. Data for ecoregions of the United States and Canada are derived from the Biota of North America Program databases developed by Kartesz and Meacham (1999). The estimates for Eurasian ecoregions may be comparatively higher than values for the Americas because the former typically encompass biogeographic areas that are broader in scope (i.e., they include mixed-conifer and broadleaf forest habitats) than ecoregions delineated for the Americas (WWF/IUCN, 1994–1997; Mittermeier et al., 1999).

Ecoregion	Species richness	Endemism
Nearctic		
Southeastern Conifer Forests	3095	>201
Sierra Nevada Forests	2373	51–75
Arizona Mountains Forests	2204	76–110
South Central Rockies Forests	1933	51–75
Klamath–Siskiyou Forests	1859	111–151
Piney Woods Forests	1729	4–10
North Central Rockies Forests	1695	21–50
Colorado Rockies Forests	1626	76–110
Middle Atlantic Coastal Forests	1488	11–20
Okanogan Forests	1355	1–3
Cascade Mountain Leeward Forests	1328	11–20
North Cascades Forests	1325	4–10
Central and Southern Cascades Forests	1296	21–50
Eastern Cascade Forests	1224	21–50
Northern California Coastal Forests	1212	11–20
Blue Mountain Forests	1134	21–50
Wasatch and Uinta Montane Forests	1109	51–75
Central Pacific Coastal Forests	1109	11–20
Puget Lowlands Forests	1100	1–3
Great Basin Montane Forests	1043	21–50
Fraser Plateau and Basin Complex	1012	0
Florida Sand Pine Scrub	951	21–50
Northern British Columbia Mountain Forests	909	0
Northern Transitional Alpine Forests	876	0
Alberta/British Columbia Foothill Forests	740	1–3
Alberta Mountain Forests	660	1–3
Northern Pacific Coastal Forests	615	1–3
Queen Charlotte Islands	459	1–3
Atlantic Coastal Pine Barrens	632	1–3
Neotropics		
Valdivian Temperate Rainforests	463	>33
Palearctic		
Caucasus Mountains	~6300	~1600
Middle Asia Mountains*	~5500	~1500
Pyrenees	~3500	~200
Balkan–Rhodope Mountains	~3000	~900
Alps	~3000	~350
Carpathians	~2000	~100
Central China Mixed-Conifer Forests	~1900	?
Eastern Himalayan Temperate Conifer Forests	~1500	?

* Kopetdag, Tienshan, Pamiro-Alai, Pamir, Dzhungarian Alatau.

phenomena. Ecoregions that contain extensive intact habitats and large vertebrate assemblages were recognized. Also considered were the long-distance migrations of larger terrestrial vertebrates such as caribou or wildebeest, and the tremendous seasonal fish migrations and fish frugivory in the flooded forests of the Amazon (varzea forests) (Goulding, 1980; Goulding et al., 1996). Such phenomena were once widespread but are now rare due to the prevalence of human disturbance around the world. This is the only situation where we consider global patterns within the context of threats. Otherwise,

Table 3. Actual or estimated vascular plant species richness and endemism (expressed as species number) of some tundra ecoregions or regions based on data from WWF/IUCN (1994), Ricketts et al. (1999), and J. T. Kartesz (pers. comm.).

Ecoregion or region	Species richness	Endemism
Nearctic		
Pacific Coastal Mountain Icefields	792	0
Alaska/St. Elias Range Tundra	747	4–10
Interior Yukon/Alaska Alpine Tundra	617	4–10
Brooks/British Range Tundra	593	1–3
Ogilvie/MacKenzie Alpine Tundra	589	4–10
Arctic Foothills Tundra	580	0
Beringia Lowland Tundra	553	0
Arctic Coastal Tundra	539	1–3
Beringia Upland Tundra	538	1–3
Low Arctic Tundra	497	0
Aleutian Islands Tundra	388	4–10
Middle Arctic Tundra	371	1–3
Torngat Mountain Tundra	286	0
High Arctic Tundra	245	0
David Highlands Tundra	216	0
Baffin Coastal Tundra	135	0
Palearctic		
Chukotsky Peninsula	939	~50
Taimyr Peninsula	240	5

the Global 200 emphasizes biodiversity features that were in place prior to major human impacts of natural habitats and species populations.

Both ecological and evolutionary phenomena are a critical, but widely overlooked, aspect of biodiversity conservation. Unusual evolutionary phenomena such as the extraordinary adaptive radiations seen in Hawaiian plants, birds, and insects, the radiation of Galápagos finches, the radiation of cichlids in Rift Valley lakes of Africa, also elevated some ecoregions to the Global 200. While evolutionary or ecological phenomena occur in every ecoregion, we highlight those that are recognized as exceptional in global comparisons.

GLOBAL RARITY

All ecoregions in globally rare biomes were considered priorities. We elevated ecoregions to Global 200 status if their biome or major habitat type was represented in fewer than eight distinct regions around the world. Examples of rare biomes include the six Mediterranean woodlands, forests, and scrub, all of limited area. Temperate rain forest ecosystems (a major habitat) occur in seven relatively localized areas around the world. Paramos, or wet tropical alpine shrublands, occur in only a few areas of the northern Andes and Central America, a few East African mountain ranges, and in New Guinea. For this criterion, we counted only naturally occurring rarity, although human-induced rarity is an important condition to assess when developing conservation strategies.

INTACTNESS

For ecoregions in the same biome that were assessed at a similar level of biological importance, we selected the ecoregions that had relatively more intact habitats and biotas (see conservation status below).

REPRESENTATION

Ecoregions were also elevated to Global 200 status if they were the best example of their biome within a realm in situations where no other ecoregion had been selected due to its outstanding biodiversity. In this selection we emphasized those ecoregions that harbored the richest or most endemic biotas, or had the most intact natural ecosystems if biological importance was similar among candidates.

The Global 200 focuses on biological values as the critical first step in setting global conservation priorities. There are many other factors that may be used in the prioritization process. We purposefully did not use ecological function, conservation feasibility (i.e., political, social, economic, cultural factors), or human utility as discriminators to iden-

tify the Global 200 as these features are either difficult to measure or are highly fluid. The development and implementation of ecoregion strategies, however, require careful attention to ecological function and non-biological factors.

The recognition of remaining wild animal migrations and other contemporary ecological phenomena is the only criterion where human impacts to the environment are recognized, because areas of extinguished phenomena are ignored. Otherwise, the Global 200 emphasizes biodiversity features that were in place prior to major human impacts on natural habitats and species populations.

Conservation Status of the Global 200 Ecoregions

Ecoregions vary greatly not only in their biological distinctiveness, but also in their conservation status. Conservation status represents an estimate of the ability of an ecoregion to maintain viable species populations, to sustain ecological processes, and to be responsive to short- and long-term environmental changes. Conservation status assessments of the Global 200 ecoregions were based on landscape or aquascape-level criteria, such as total habitat loss, the degree of fragmentation, water quality, and estimates of future threat. From a practical perspective, a measure of conservation status can dictate the urgency, kinds of conservation activities, and level of effort needed among ecoregions or biomes. Conservation status can also indicate areas with relatively high opportunity for far-reaching conservation measures.

We estimated the conservation status of ecoregions specifically to enable us to make decisions about elevating ecoregions when the similarity of their biodiversity features made discrimination challenging. Conservation status was also used to assess broad trends in threats among different regions and biomes. Again, we drew heavily from regional conservation assessments to estimate conservation status.[7] For the Global 200, we classified ecoregions into one of three broad categories: critical/endangered, vulnerable, or relatively stable/relatively intact over the next 40 years. For terrestrial ecoregions, the most prominent contributor to conservation status is habitat loss, followed by the size of remaining habitat blocks, degree of fragmentation, degree of degradation, and degree of protection (see Appendix 2). Weightings for factors varied by biome for freshwater and marine ecoregions.

The Global 200 Ecoregions

We identified 238 ecoregions whose biodiversity and representation values are outstanding or significant on a global scale (Table 1). They represent the terrestrial, freshwater, and marine realms, and the 30 biomes nested within these realms. Among the three realms, 142 (60%) are terrestrial, 53 (22%) are freshwater ecoregions, and 43 (18%) are marine. Terrestrial ecoregions outnumber those of the other realms largely because there is more localized endemism in terrestrial than in marine biotas. Gaps in biogeographic information for freshwater and marine biodiversity also account for some of the variation.

TERRESTRIAL REALM

Tropical and subtropical moist forests

Among the 14 terrestrial biomes, the largest number of Global 200 ecoregions falls within the tropical and subtropical moist forests biome (50 ecoregions or 35% of all terrestrial ecoregions) (Table 1). The high number of ecoregions reflects the biological richness and complexity of tropical moist forests. Although there are more tropical moist forest ecoregions in the Indo-Malayan Biogeographic realm (17) than in the Neotropics (12), this is partly due to the archipelagic distributions of Asian tropical moist forests and their characteristic biotas (Whitmore, 1986, 1990; Whitten et al., 1987a, 1987b, 1996; Wikramanayake et al., 2001). Four of the Asian tropical moist forests are small island systems, and the original extent of all of the Asian ecoregions fits easily within the area covered by western Amazonian moist forests.

The most diverse terrestrial ecoregions occur in the Western Arc forests of the Amazon Basin, with close rivals in the Atlantic Forest ecoregion of Brazil, the Chocó-Darién ecoregion of northwestern South America, Sumatra, and Peninsular Malaysia and northern Borneo forest ecoregions. The montane forest biotas of the Northern Andes are remarkable for their globally high rates of beta-diversity and extraordinary local endemism (Terborgh & Winter, 1983; ICBP, 1992; Hamilton et al., 1995; Wege & Long, 1995; WWF/IUCN, 1994–1997). The forests of the Guayanan region and Cuba are known for their pronounced endemism and unusual

[7] IUCN (1991, 1992), Krever et al. (1994), BSP et al. (1995), Dinerstein et al. (1995), Harcourt et al. (1996), MacKinnon & Bunting (1996), Bryant et al. (1997), Dinerstein et al. (1995), Dobson et al. (1997), Ricketts et al. (1999), Abell et al. (2000), Bryant et al. (2000), Conservation International (2000), Wikramanayake et al. (2001), Burgess et al. (in press).

biogeographic relationships (Whitmore & Prance, 1987; Borhidi, 1991; Dinerstein et al., 1995; Steyermark et al., 1995; Hedges, 1996). The forests of the Greater Antilles also are notable for a number of relict mammals, such as solenodons and hutias. The Congolian coastal forests are likely the most diverse in the Afrotropics, although diversity information is scarce for several ecoregions in the central Congo Basin (Oates, 1996; Kingdon, 1997; Burgess et al., in press). The Guinean moist forests support many species not found in the Central African region (IUCN/UNEP, 1986a; IUCN, 1990; Martin, 1991; IUCN, 1992; Mittermeier et al., 1999). The Albertine Rift montane forests are extremely rich for some taxa, such as birds, and have a high degree of endemism (Collar & Stuart, 1988; Kingdon, 1989; WWF/IUCN, 1994). The distinctiveness of the Eastern Arc montane and East African coastal forests is attributable to their great age and isolation (Hamilton & Bensted-Smith, 1989; Lovett & Wasser, 1993; Hamilton et al., 1995; Burgess et al., in press). Madagascar forests and shrublands are also highly distinctive on global scales, especially at higher taxonomic levels (Nicoll & Langrand, 1989; Preston-Mafham, 1991; WWF/IUCN, 1994). Tropical moist forests of New Guinea are highly distinctive (Brooks, 1987; Flannery, 1990, 1994; WWF/IUCN, 1994; Mittermeier et al., 1996; Wikramanayake et al., 2001), although Australian moist forests do share many affinities with New Guinea. The long-isolated forests of New Caledonia are exceptionally unusual, with so many endemic and relict higher taxa and species that the island is considered the 'Madagascar of the Pacific.' The forests of Sulawesi are noted for their regionally high degree of endemism in a range of taxa, a phenomenon also seen in the Philippine moist forests and in the Lesser Sundas semi-evergreen forests (IUCN/UNEP, 1986b; IUCN, 1991; ICBP, 1992; Stattersfield et al., 1998; Wikramanayake et al., 2001). The Western Ghats and southwestern Sri Lankan moist forests are distinctive due to their isolation and stability of conditions over millions of years. Tropical moist forests on oceanic islands are often highly distinctive due to high rates of endemism, extraordinary radiations of taxa and adaptive radiation, and relictual or unique higher taxa (Dahl, 1986; Mitchell, 1989; Johnson & Stattersfield, 1990; Flannery, 1994; WWF/IUCN, 1994; Wagner & Funk, 1995).

Tropical and subtropical dry forests

The most diverse dry forests in the world occur in southern Mexico and in the Bolivian lowlands (Gentry, 1993; Parker et al., 1993; Bullock et al., 1996). The dry forests of the Pacific Coast of northwestern South America support a wealth of unique species due to their isolation (Parker & Carr, 1992; WWF/IUCN, 1994; Bullock et al., 1996). The subtropical forests of Maputaland-Pondoland in southeastern Africa are diverse and support many endemics (Cowling & Hilton-Taylor, 1994; WWF/IUCN, 1994). The dry forests of central India and Indochina are notable for their diverse large vertebrate faunas (Corbett & Hill, 1992; Stewart-Cox, 1995). Dry forests of Madagascar and New Caledonia are globally distinctive because of their high number of relictual taxa and extreme endemism (IUCN/UNEP/WWF, 1987; Preston-Mafham, 1991; WWF/IUCN, 1994; Wikramanayake et al., 2001).

Tropical and subtropical coniferous forests

Mexico harbors the world's richest and most complex subtropical coniferous forests (Perry, 1991; Peterson et al., 1993; Ramamoorthy et al., 1993; WWF/IUCN, 1994). The conifer forests of the Greater Antilles contain many endemics and relictual taxa (Borhidi, 1991). Subtropical conifer forests of Indochina are incorporated into the dry and moist forests of the region.

Temperate broadleaf and mixed forests

Temperate broadleaf and mixed forests are richest in central China and eastern North America, with other globally distinctive ecoregions occurring in the Caucasus, the Himalayas, southern Europe, and the Russian Far East (Table 2) (Zhao et al., 1990; Martin et al., 1993; Oosterbroek, 1994; WWF/IUCN, 1994; MacKinnon & Hicks, 1996; Ricketts et al., 1999).

Temperate coniferous forests

Temperate rain forests only occur in seven regions around the world—the Pacific Northwest, the Validivian forests of southwestern South America, the rain forests of New Zealand and Tasmania, the Northeastern Atlantic (small, isolated pockets in Ireland, Scotland, and Iceland), southwestern Japan, and those of the eastern Black Sea (Kellogg et al., 1992; WWF/IUCN, 1994). Forest communities dominated by huge trees (e.g., giant sequoia, *Sequoiadendron gigantea* (Lindl.) J. Buchholz; redwood, *Sequoia sempervirens* (D. Don) Endl.; mountain ash, *Eucalyptus regnans* F. Muell.) are unusual ecological phenomena that are found only in western North America, southwestern South America, and in the Australasian region in such areas as

southeastern Australia and northern New Zealand. The Klamath–Siskiyou ecoregion of western North America harbors diverse and unusual assemblages and displays notable endemism for a number of plant and animal taxa. The Valdivian forests of Chile are notable for their diversity of tree genera, many of which are monotypic and have Gondwanaland origins. These long-isolated forests have many other unusual taxa and unique communities.

Boreal forests and taiga

Low species richness and endemism are characteristic of circumboreal and circumpolar ecoregions (USSR Academy of Sciences, 1988), thus the presence of intact ecological phenomena denoted outstanding ecoregions. Large-scale migrations of caribou, or reindeer (*Rangifer tarandus*), and intact predator assemblages can still be found in some regions. For example, the Northern Cordillera boreal forests of Canada have been called the Serengeti of the Far North due to their abundance and diversity of large vertebrates (Ricketts et al., 1999). Extensive tracts of boreal forest and taiga still exist in the northern Nearctic and Palearctic, the largest expanses being in central and eastern Russia (Stewart, 1992; Krever et al., 1994). This biome also enjoys relatively unaltered natural disturbance regimes, an increasingly rare situation in other biomes.

Tropical and subtropical grasslands, savannas, and shrublands

In many parts of the tropics large mammal faunas have evolved to take advantage of the productive grasses and browse typical of this biome. These large mammal faunas are richest in African savannas and grasslands. Presently the most intact assemblages occur in East African acacia savannas and Zambezian savannas comprised of mosaics of miombo, mopane, and other habitats (McClanahan & Young, 1996). Large-scale migration of tropical savanna herbivores, such as wildebeest (*Connochaetes taurinus*) and zebra (*Equus zebra*), are continuing to decline through habitat alteration and hunting. Only in East Africa, the central Zambezian region, and in the Sudd region (Uganda kob or *Kobus kob*) do sizable migrations still persist. Many of the extraordinary migrations of the Guinean and Sahelian savannas have disappeared. Sahelian ecoregions support a large number of endemic rodent species, while the Somalian bushland and thickets harbor a concentration of endemic mammals, from rodents to antelopes. Both the Cerrado and the Llanos are noted for complexity of habitats and the unusually high levels of endemism and beta diversity in plants for tropical savannas. The tropical savannas of northern Australia and southern New Guinea support distinctive communities with several pockets of endemism for a range of taxa (Stattersfield et al., 1998).

Temperate grasslands, savannas, and shrublands

The vast expanses of grass in North America and Eurasia once sustained vast migrations of large vertebrates such as buffalo (*Bison bison*) and saiga (*Saiga tatarica*). Such extraordinary phenomena now occur only in isolated pockets, such as on the Daurian Steppe (Krever et al., 1994; Hilbig, 1995; Finch, 1996). The extraordinary floral communities of the Eurasian steppes and the North American Great Plains have been largely extirpated through conversion to agriculture. Nearly 300 different plant species can occur on a few hectares of North American tallgrass prairie. The Patagonian steppe and grasslands are notable for endemic higher taxa for mammals.

Flooded grasslands and savannas

Some globally outstanding flooded savannas and grasslands occur in the Everglades, Pantanal, Sahelian flooded savannas, Zambezian flooded savannas (including the Okavango Delta), and the Sudd. The Everglades are the world's largest rain-fed flooded grassland on a limestone substrate. The flooded savannas and grasslands selected are generally the largest complexes in each region. Another extraordinary inland delta, the Mamberamo River inland delta, is captured within the montane forests of the New Guinea ecoregion.

Montane grasslands and shrublands

The paramos of the northern Andes are the most extensive examples of this biome. Paramo ecosystems occur in only a few other localities in the tropics. The heathlands and moorlands of East Africa (e.g., Mt. Kilimanjaro, Mt. Kenya, Rwenzori Mts., Ethiopian Highlands), Mt. Kinabalu of Borneo, and the Central Range of New Guinea are all limited in extent, extremely isolated, and support highly endemic plants and animals. A characteristic feature of many tropical paramos is the presence of large rosette plants from a variety of plant genera, such as *Lobelia* (Africa), *Puya* (South America), *Cyathea* (New Guinea), and *Argyroxiphium* (Hawaii)—these plant forms can reach elevations of 4500–4600 m above sea level. Drier, yet distinctive, subtropical montane grasslands, savannas, and woodlands in-

clude the Ethiopian Highlands, the Zambezian montane grasslands and woodlands, and the montane habitats of southeastern Africa (Werger, 1978; White, 1983; Huntley, 1989, 1994; Timberlake & Müller, 1994; WWF/IUCN, 1994). The montane grasslands of the Tibetan Plateau still support relatively intact migrations of Tibetan antelope (*Pantholops hodgsoni*) and kiang, the Tibetan wild ass (*Equus hemionus*). The puna grasslands of the high Andes support over 30 species of endemic rodents (45 total species).

Tundra

Tundra ecoregions were selected primarily because of extraordinary seasonal concentrations of breeding waterfowl and shorebirds, and caribou (Stewart, 1992; Krever et al., 1994; Ricketts et al., 1999). Relatively intact tundra ecoregions were chosen, wherever possible. The Chukotsky tundra ecoregion is unusual with nearly 50 endemic plant species (Knystautas, 1987; USSR Academy of Sciences, 1988; WWF/IUCN, 1994).

Deserts and xeric shrublands

The Namib–Karoo deserts of southwestern Africa support the world's richest desert floras (Cowling & Hilton-Taylor, 1994; Maggs et al., 1994; WWF/IUCN, 1994), while the Chihuahuan Desert and central Mexican deserts are a close second and are the richest Neotropical deserts (Cowling et al., 1989; Hernandez & Barcenas, 1995; Ricketts et al., 1999). Australian deserts support the richest reptile faunas. The Carnavon Xeric Scrub of western Australia is a regional center of endemism for a range of taxa. Unusual desert communities dominated by giant columnar cacti occur in the Sonoran and Baja Deserts of North America (Brown, 1994), while the spiny thickets of southwestern Madagascar are globally unique in terms of structure and taxa. Some Baja California communities are partially convergent in structure with the Madagascar thickets. The Atacama Desert ecoregion of western South America (including the adjacent transition area of the Monte/Puna/Yungas) and the Horn of Africa deserts were recognized as some of the more outstanding regional centers of richness and endemism. The Central Asian deserts, while not as rich as Afrotropical or Neotropical deserts, are representative of the region's deserts with diverse reptile and mammal faunas.

Mediterranean forests, woodlands, and scrub

All five Mediterranean-climate ecoregions are highly distinctive, collectively harboring 20 percent of the Earth's plant species (Cody, 1986; Kalin Arroyo et al., 1995; Picker & Samways, 1995). Phytogeographers consider the Fynbos as a separate floral kingdom because 68% of the 8600 vascular plant species crowded into its 90,000 km^2 are endemic and highly distinctive at several taxonomic levels (Cowling et al., 1989, 1996; Cowling & Hilton-Taylor, 1994). In terms of species densities, this is equivalent to about 40 percent of the plant species of the United States and Canada combined, found within an area the size of the state of Indiana (N. Myers, pers. comm.). The Fynbos and Southwest Australia shrublands have floras that are significantly more diverse than the other ecoregions, although any Mediterranean shrubland is still rich in species and endemics relative to other non-forest ecoregions (Cowling et al., 1996; Oosterbroek, 1994).

Mangroves

The diversity of mangroves in the Indo-West Pacific (IWP) region is much greater than those of the Atlantic–Caribbean–East Pacific (ACEP) region—the former supporting 17 genera and 40–42 species of true mangroves and the latter having only 4 genera and 7 species (MacNae, 1968; Lacerda, 1993; Olson et al., 1996; Spalding et al., 1997; Ricklefs & Latham, 1993). A single site in the ACEP typically contains 3 or 4 true mangrove species, while 30 species have been recorded from one locality in the IWP region (Ricklefs & Latham, 1993). Mangrove forests on the western coast of Madagascar support a number of endemic bird species that are endangered. The mangrove swamps and forests of the Indo-Malayan and Australasian realms are the world's most extensive. South and Southeast Asia alone contain 42% of the total area of the world's mangroves (Spalding et al., 1997). The Sundarbans are the largest contiguous mangrove forest in the world. The vast floodplains of New Guinea also support extensive mangrove swamps unrivaled elsewhere in the world.

If all of the marine, freshwater, and terrestrial species that occur in mangroves are considered, these seemingly simple forests can be considered as one of the more diverse ecosystems in the tropics. Mangroves are keystone habitats in the sense that they have an inordinately strong influence on species populations and ecosystems well beyond their limited area. In addition to providing habitat and resources to a wide range of species, mangrove forests and swamps also protect inland habitats and shorelines from damage by damping storm waves and tidal action. Mangroves filter silt and pollutants

from terrestrial runoff that would otherwise damage seagrass beds and coral reefs.

FRESHWATER REALM

Large rivers

Faunas adapted to high-flow regimes of large rivers are uncommon and best developed in the Yangtze, Colorado, and lower Congo Rivers. A relatively small area of rapids in the latter region supports 22 endemic species of fish that are rapid specialists (Lowe-McConnell, 1987). The Mekong, Congo, Paraná, and Amazon–Orinoco Rivers harbor the four great large tropical river fish faunas (Mori, 1936; Roberts, 1975; Hocutt & Wiley, 1986; Lowe-McConnell, 1987; Kottelat & Whitten, 1996). The waters of the Lower Yangtze and Mississippi Rivers contain outstanding examples of large-river fishes, amphibians, reptiles, and invertebrates, including relicts and many endemics (Abell et al., 2000).

Large river headwaters

Species, assemblages, and processes in headwater areas are distinct from those of their larger mainstems. The Mississippi Piedmont, Guayanan highlands, Upper Amazon, Upper Paraná, Brazilian Shield, and Congo Basin Piedmont harbor a tremendous array of species, including numerous endemics adapted to life in these waters. In turn, these river systems ultimately feed a number of the world's largest and richest rivers (Hocutt & Wiley, 1986; Kottelat & Whitten, 1996; Thieme et al., in press). The most diverse vertebrate assemblages on Earth occur in freshwater communities of the Amazon and the Orinoco River basins. Over 3000 species of fish are estimated to occur in the Amazon Basin alone (Goulding, 1980).

Large river deltas

Delta complexes of several large temperate and polar rivers are identified, including the Mesopotamian, Volga, and Lena River deltas. The Niger River delta, the most extensive river delta in Africa, is characterized by high species richness (Wetlands International and The World Bank, 1996; Thieme et al., in press). The extensive deltas of the Orinoco and Amazon Rivers are encompassed in their respective large-river ecoregions (see above).

Small river basins

The Mississippi River embayment, the Mobile River basin, and numerous coastal streams and rivers of southeastern North America together support one of the Earth's richest temperate freshwater biotas (Hocutt & Wiley, 1986; Hackney et al., 1992; Abell et al., 2000). The headwater streams and rivers of the Yangtze River in central China are also extremely diverse (recognized as a large river biome in this analysis) (Mori, 1936; Nichols, 1943; Taki, 1975). Secondary centers of temperate diversity occur in the rivers and streams of southeastern North America, the western coast of North America, and the Russian Far East (Zhadin & Gerd, 1961; Lee et al., 1980; Hocutt & Wiley, 1986; Groombridge & Jenkins, 1998; Abell et al., 2000). Several freshwater biotas on islands are highly distinctive, including those of Madagascar, New Guinea, the Greater Sundas, the Greater Antilles, Sri Lanka, and New Caledonia (IUCN/UNEP/WWF, 1987; Zakaria-Ismail, 1987, 1994; Allen, 1991; Preston-Mafham, 1991; Oberdorff et al., 1995). The Southwest Australian Rivers and streams ecoregion is a center of endemism, while also harboring a number of primitive higher taxa and several species with highly unusual freshwater life histories (McDowall, 1996; State of the Environment Advisory Council, 1996). Rivers and streams along the Gulf of Guinea harbor some of the richest and most endemic riverine freshwater biotas in Africa (Kingdon, 1989; Lévêque et al., 1992; Lévêque, 1997; Thieme et al., in press). The Salween River of Southeast Asia is recognized for its rich and endemic freshwater fish fauna (WCMC, 1992). The rivers and streams of New Guinea, including the inland delta of the Mamberamo River of New Guinea, support a large number of unusual and endemic species and higher taxa.

Large lakes

The Global 200 also identifies the most outstanding examples of diverse and endemic freshwater faunas in large lakes found in temperate and tropical regions, many displaying extraordinary species flocks and adaptive radiations in fish taxa. Some particularly notable lake biotas include those of the African Rift Lakes and Lake Tana in Ethiopia, Lake Baikal, Lake Biwa of southern Japan, the high-altitude lakes of the Andes, and the highland lakes of Mexico (Myers, 1960; Roberts, 1975; Hocutt & Wiley, 1986; Allen, 1991; Stiassny et al., 1992; WCMC, 1992; Nagelkerke et al., 1995; Kottelat & Whitten, 1996; Olson et al., 1999; Thieme et al., in press).

Small lakes

Similarly, a number of smaller lakes around the world host extraordinary expressions of freshwater

biodiversity. Lake Kutubu and Lake Sentani of New Guinea, Yunnan Lakes and Streams, Mexican Highland Lakes, the Cameroon Crater Lakes, Lake Lanao of the Philippines, Lake Inle in Myanmar (Burma), and the Central Sulawesi Lakes have been selected for their globally outstanding biodiversity features.

Xeric basins

Ephemeral streams, rivers, and lakes, and permanent springs characterize ecoregions in this biome. Low richness and high endemism in fish and invertebrates (e.g., molluscs) is typical of the Chihuahuan, Anatolian, and Central Australian freshwater ecoregions (Hocutt & Wiley, 1986; Balik, 1995; Abell et al., 2000). The Cuatro Ciénegas spring and pool complex in the Chihuahuan Desert is globally unique in its high richness, extreme endemism, and unusual evolutionary adaptations (Contreras-Balderas, 1978; Hocutt & Wiley, 1986). Freshwater habitats in the Anatolian region of Turkey support many endemic species (Balik, 1995).

MARINE REALM

The distribution of marine biodiversity varies widely throughout ocean basins (Briggs, 1974; Elder & Pernetta, 1991; Angel, 1992, 1993; Clarke, 1992; Kendall & Aschan, 1993; Kelleher et al., 1995; Groombridge & Jenkins, 1996; Ormond et al., 1997). The abundance and diversity of most taxa tend to be highest near continental and island margins that are less than 2000 m deep (Ray, 1991; Johannes & Hatcher, 1986; Gray, 1997). These areas experience nutrient enrichment from upwelling processes and terrestrial runoff (Ray, 1988; Norse, 1995). Areas where significant upwelling occurs are often extraordinarily productive in tropical, temperate, and polar regions. Within biomes, species richness and endemism also vary enormously around the globe.

Current biogeographic data suggest that species endemism tends to be less pronounced in marine ecosystems than in terrestrial or freshwater ecoregions, but several regional centers of endemism are recognized, including the southern coast of Australia, New Caledonia, Lord Howe and Norfolk Islands, the northern coast of South America, the Yellow and East China Seas, the Red Sea, the Mediterranean Sea, the Sea of Cortez, the Great Barrier Reef, and tropical Pacific Islands such as Hawaii, the Marquesas, the Tuamotus and Societies, and Easter Island (Robbins, 1991; Lieske & Myers, 1996; Vernon, 1995; Groombridge & Jenkins, 1996). In general, marine ecoregions associated with isolated islands and enclosed seas tend to display pronounced endemism (Kelleher et al., 1995; Groombridge & Jenkins, 1996).

We categorized the marine realm into 10 biomes. Pelagic (trades and westerlies), abyssal, and hadal biomes, however, were not assessed for the Global 200 marine analysis because of the large scale of these units compared to other Global 200 ecoregions, the lack of consensus on their classification, and the limited biodiversity information for these ecosystems (see Gage & Tyler, 1991; Grassle, 1991; Grassle & Maciolek, 1992). Large biogeographic units have been identified for pelagic and abyssal biotas (e.g., Brinton, 1962; Angel, 1993; Longhurst, 1998; Pierrot-Bults, 1997; Vinogradova, 1997), but their scale is several orders of magnitude greater than most Global 200 ecoregions. These larger units may be biogeographically and dynamically appropriate for open ocean environments. The vast size and dynamic nature of these biomes precluded delineating biogeographic subunits at an appropriate level of resolution for the Global 200. Pelagic species are noted for widespread distributions, while the few ocean trench surveys that are available suggest many species are endemic to single trenches. The paucity of species data for these ecosystems also reduces our confidence to undertake comparative analyses.

Polar

The Weddell Sea and Peninsular Antarctica were identified as the most productive and diverse ecoregions of the Antarctic large marine ecosystem. The Bering, Beaufort, and Chukchi Seas and Barents–Kara Seas ecoregions are arguably the two most diverse and productive Arctic marine ecosystems (USSR Academy of Sciences, 1988; Reeves & Leatherwood, 1994). Marine ecosystems near southern Greenland require further evaluation.

Temperate shelf and seas

Some of the most productive marine ecosystems occur in the Grand Banks and New Zealand plus the Patagonia ecoregions. The South Australian coastal waters are remarkable for unusually high levels of endemism in invertebrates and some groups of fish, in addition to the diverse marine mammal assemblage found there. Two of the world's largest temperate estuaries, the Chesapeake and Delaware Bays, and the Northeast Atlantic Shelf are elevated to the Global 200 due to their size, productivity, and habitat diversity. Some of the most distinctive enclosed temperate seas, the Mediter-

ranean Sea and the Yellow–East China Seas, are recognized in the Global 200.

Temperate upwelling

Highly productive and diverse coastal upwelling areas occur along the West Coast of North America where the California Current moves southward. Along the southwest coast of Africa the Benguela Current exhibits similar dynamics.

Tropical upwelling

The Humboldt Current along the West Coast of South America and the Canary Current along the West Coast of Africa bring rich nutrients to the sea surface where they support highly productive marine systems. Important tropical upwelling and current areas also occur in the Panama Bight ecoregions.

Tropical coral

Southeast Asian seas support more than 450 species of hard (scleractinian) corals, the western Indian Ocean around 200, and the Caribbean only 50 species (Vernon, 1995). Variation in reef fish and non-coral invertebrate diversity follows a similar biogeographic pattern (McAllister et al., 1994; Lieske & Myers, 1996). Overall, the coral reef communities of the central Indo-Pacific seas are the most diverse in the world, with the Sulu, Sulawesi, Banda, and Coral Sea ecoregions being the most diverse on Earth (Vernon, 1995; Lieske & Myers, 1996). The largest barrier reef in the world is the Great Barrier Reef. Other world-class barrier reefs include the barrier reefs of New Caledonia, the Mesoamerican and Bahamian barrier reefs, and the large barrier reefs of Fiji. The largest coral atoll complexes occur in the Maldive-Lakshadweep ecoregion of the central Indian Ocean and in the Tuamotus of the central Pacific.

Conservation Status of Ecoregions

Among all terrestrial Global 200 ecoregions (142 in total), 75 ecoregions (53%) are considered critical or endangered, 39 ecoregions (27%) vulnerable, and 28 ecoregions (20%) relatively stable or intact (Table 1). Terrestrial ecoregion boundaries do not reflect the extensive habitat loss, fragmentation, and degradation that have occurred in many of the terrestrial ecoregions. In ecoregions that have been dramatically altered, characteristic species and communities survive only in the few remaining small blocks of habitat (e.g., Collar & Stuart, 1988; Dinerstein et al., 1995). Among the terrestrial biomes, ecoregions falling within the tropical and subtropical dry broadleaf forests, temperate grasslands, Mediterranean shrublands, and temperate broadleaf and mixed forests are the most threatened. Virtually all biotas on small islands are vulnerable or critical/endangered due, in large part, to their limited habitat area and extreme sensitivity to anthropogenic disturbance and alien species (Raven, 1988; Wilson, 1988, 1992; WCMC, 1992; Sujatnika et al., 1995; Brooks et al., 1997; Reaka-Kudla et al., 1997). Island ecoregions are projected to experience a wave of extinctions over the next two decades given the fragility of island ecosystems, the sensitivity and endemicity of island species, and the severe threats native island biotas face worldwide. Mangrove habitats are threatened worldwide from a range of threats including clearing and channelization for shrimp ponds, aquaculture, and agriculture, the extraction of timber and fuelwood, pollution, and habitat loss due to urban and industrial expansion.

Assessment of conservation status for freshwater ecoregions in North America and South America was based on existing regional analyses (Abell et al., 2000; Olson et al., 1999). In Africa and Europe, analyses currently under way (Thieme et al., in press) provided the basis for rankings presented here. In areas where no regional assessment has been undertaken, review of relevant literature facilitated decisions on the levels of threat faced by native biotas. Worldwide, freshwater organisms represent a disproportionate number of endangered species; thus, it is not surprising that so many freshwater ecoregions received a critical rating in the assessment. In particular, seasonally flooded forests, cataracts, and freshwater communities in xeric areas, are endangered worldwide (Goulding et al., 1996; Abell et al., 2000; Olson et al., 1999). Moreover, most temperate freshwater biotas are threatened by invasion of exotics, pollution, dams, and habitat degradation. Among the 53 freshwater ecoregions 31 (58%) were deemed to be critical or endangered, 10 (19%) were assessed as vulnerable, and only 12 (23%) were assessed as relatively stable.

The individual status of marine ecoregions was estimated through review of the literature and consultations with regional specialists. Twelve marine ecoregions (29%) were considered relatively stable or intact, while another 12 (29%) were considered critical or endangered. In marine biomes, upwelling areas are heavily overfished, enclosed seas are degraded, and coral reefs and mangroves are severely affected by habitat destruction, degradation, and overfishing around the world (Sherman et al., 1990;

Suchanek, 1994; Kelleher et al., 1995; Bryant et al., 1995; Olson et al., 1996; Ormond et al., 1997). Increasingly rising sea surface temperatures from global warming may endanger all coral reef ecoregions within several decades.

Degree of Overlap of Terrestrial, Freshwater, and Marine Global 200 Ecoregions

The linkages among terrestrial, freshwater, and marine conservation are often overlooked. Among the Global 200, 33 (23%) of the 143 terrestrial ecoregions overlap extensively with freshwater ecoregions (i.e., more than 50% of the original extent of the terrestrial ecoregion is covered by a freshwater unit). Thirty-four (23%) of the terrestrial ecoregions share at least 50% of their coastline with a marine ecoregion. Ten (6%) of the terrestrial ecoregions do both, overlapping extensively with a freshwater ecoregion and sharing at least 50% of their coastline with a marine ecoregion. The terrestrial ecoregions of this third group are the Madagascar dry forests, Congolian coastal forests, Greater Antilles moist forests, Pacific temperate rain forests of North America, Queensland tropical moist forests, southeastern Australia *Eucalyptus–Acacia* forests, New Caledonia moist forests, New Caledonia dry forests, New Guinea lowland forests, Sulawesi moist forests, Philippine moist forests, Northeast Borneo/Palawan moist forests, and Russian Far East temperate forests. Carefully designed conservation activities in these 13 units could ultimately affect 39 ecoregions.

The Global 200 as a Conservation Tool

The Global 200 is based on the best available information and biological insights. As new interpretations of biogeography and better information on the distribution of species and phenomena become available, we expect to periodically revise the Global 200. The present list and map incorporate a number of changes from an earlier version (Olson & Dinerstein, 1998). For example, the highly unusual freshwater biota of southwestern Australia is now recognized, and the terrestrial ecoregions of the Amazon Basin have undergone major revisions based on a recent biogeographic analysis by Silva (1998).

EXPANDING CONSERVATION GOALS

The Global 200 goes beyond the conservation targets of other prominent global priority-setting efforts by explicitly incorporating representation guidelines for biomes within realms. Biological phenomena are also important criteria used in its selection protocol. The Global 200 also emphasizes freshwater and marine biodiversity. The Hotspots analysis (Mittermeier et al., 1999; Myers et al., 2000), for example, mostly targets very large and threatened terrestrial regions with concentrations of range-restricted (locally endemic) species. The Hotspots are largely nested within the Global 200 (> 90% congruence) because both analyses emphasize exceptional levels of endemism for species and higher taxa. The Global 200 can complement hotspot analyses by corroborating the vast majority of their priority areas and, in some cases, by providing a finer resolution of the variation of biodiversity features within important regions. For example, the Madagascar Hotspot identified by Myers et al. (2000) corresponds to five separate Global 200 ecoregions and the Indo-Burma Hotspot overlaps with 14 Global 200 terrestrial and freshwater ecoregions. The Global 200 also encompasses distinct freshwater and marine hotspots and warmspots, as well as ecoregions important for their extraordinary ecological or evolutionary phenomena and their representation value. Endemic Bird Areas of the World highlights concentrations of bird species with restricted ranges (Stattersfield et al., 1998). Like hotspots, the majority of the Endemic Bird Areas are nested within the Global 200. Both Tropical Forest Wilderness Areas (Mittermeier et al., 1999) and Frontier Forests (Bryant et al., 1997) map larger landscapes of relatively undisturbed natural forests around the world. Although the Global 200 does not specifically employ forest wilderness as a discriminator, again there is extensive overlap with these wilderness areas because such areas often harbor rich assemblages of species and endemics, and unusual phenomena such as intact predator-prey systems.

OTHER CONSERVATION TARGETS

Other conservation targets, such as species of special concern, keystone species, habitats, and phenomena, large-scale ecological phenomena (e.g., bird, butterfly, caribou, cetacean, sea turtle migrations), wilderness areas, ameliorating climate change impacts, reducing toxins, and maintaining ecosystems with low impacts from alien species are also not directly addressed by the Global 200. Again, effective conservation within priority ecoregions and coordinated efforts among ecoregions will help achieve conservation goals for these targets.

An Ambitious Blueprint for Global Conservation

One tactical concern of the Global 200 is that it is ambitious, and that by focusing on 238 ecoregions rather than on a handful of conservation units, we run the risk of placing less emphasis on the most diverse and distinct ecoregions. In response, we maintain that the broad geographic reach of the Global 200 makes almost every nation on Earth a stakeholder in a global conservation strategy. From the global scale to regional and national-level conservation strategies, the Global 200 lends weight to shared priorities and provides a global perspective for lobbying efforts by local conservation groups. The Global 200 also can help major development agencies better recognize and mitigate the effects of projects that result in land use change, or forego development activities in particularly important and sensitive ecoregions.

The targets of the Global 200—representation, outstanding ecoregions, and ecological phenomena—are all essential elements of a global conservation strategy. The conservation community should not shrink from this ambitious but necessary agenda. The widespread destruction of the Earth's biodiversity occurring today must be matched by a response at least an order of magnitude greater than currently exists. The Global 200 provides a necessarily ambitious template for a global conservation strategy.

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Appendix 1. Weighting and Measuring Biological Distinctiveness Criteria

The weighting and measurement of the parameters used to assess the biological distinctiveness of terrestrial ecoregions of North America are presented here to illustrate how different biodiversity features were evaluated as conservation targets and how analyses were tailored to different biomes. Comparisons among biodiversity parameters were only conducted within the set of ecoregions sharing the same biome.

Species richness*

Globally outstanding	100
High	15
Medium	10
Low	5

*Only native species were used in species counts.

Endemism

Globally outstanding	100
High	25
Medium	15
Low	5

For species richness and endemism, the total number of species that occurs within each ecoregion, and the total number of endemic species, were determined for a range of native taxa: full species of native vascular plants, land snails, butterflies, reptiles, amphibians, birds, and mammals. Species distributions were derived from published range maps and the available literature. For land snails and native vascular plants, regional experts compiled the databases. Barry Roth analyzed land snail distributions for western North America, and John Kartesz analyzed richness and endemism data for native vascular plants. A species was considered "endemic" to an ecoregion if its estimated range fell entirely within a single ecoregion (strict endemic), 75% or more of its range fell within a single ecoregion (near-endemic), or its range was less than 50,000 km^2 (range-restricted). If a species had a significant distribution outside of the United States and Canada, it was not considered as an endemic. Higher taxonomic uniqueness—e.g., unique genera or families, relict species or communities, primitive lineages—was also considered for identifying globally outstanding ecoregions from an endemism perspective.

The actual number of species and endemics for each taxon found within an ecoregion were log transformed to reduce the influence of very species-rich groups. The logs were then summed to derive a single richness and endemism score. These scores were plotted for the ecoregions within each biome and the curves broken subjectively into high, medium, and low scores. Globally outstanding scores were determined through comparisons with values for ecoregions within the same biome found throughout the world.

Unusual ecological or evolutionary phenomena

Globally outstanding	100
Regionally outstanding	5
No globally or regionally unusual phenomena	0

Examples of unusual ecological or evolutionary phenomena at global or regional scales include relatively intact, large-scale migrations of large vertebrates such as caribou, intact predator assemblages, superabundant concentrations of breeding waterfowl and shorebirds, extraordinary levels of adaptive radiations, rain-fed flooded grasslands on limestone, and conifer forests dominated by gigantic trees.

Global rarity of biome

Global rarity	100
Regional rarity	5
Not rare at global scale	0

Biomes or habitats that were considered globally rare include Mediterranean-climate forests, woodlands, and scrub, temperate rainforests, and paramo.

Total scores for determining biological distinctiveness index

The points from each criterion were summed to arrive at a final score. This score was then translated into a biological distinctiveness category as follows:

Globally outstanding	45, 50, or 55+ points
Regionally outstanding	30, 35, 40
Bioregionally outstanding	20, 25
Locally important	10, 15

Ecoregions identified as globally outstanding were subsequently compared with similar ecoregions around the world to validate their relative status.

Appendix 2. Assessing Conservation Status of Ecoregions

Conservation status measures landscape and ecosystem-level features and relates these to the ecological integrity of ecoregions, namely, how with increasing habitat loss, degradation, and fragmentation, ecological processes cease to function naturally, or at all, resiliency to disturbance declines, and major components of biodiversity are steadily eroded. We assess the conservation status of ecoregions in the tradition of IUCN Red Data Book categories for threatened and endangered species: critical, endangered, and vulnerable. For ecoregions we used the following conservation status categories: critical, endangered, vulnerable, relatively stable, and relatively intact. Throughout all of the regional analyses, the specific parameters and thresholds used for assessing conservation status were tailored to the characteristic patterns of biodiversity, ecological dynamics, and responses to disturbance of different biomes.

Terrestrial ecoregions

We present the method used to assess conservation status for the terrestrial ecoregions of North America to illustrate the approach (Ricketts et al., 1999). The relative contributions of different parameters were as follows: 40%—habitat loss, 25%—number and size of remaining blocks of intact habitat, 20%—degree of habitat fragmentation, and 15%—degree of protection. A snapshot conservation status was estimated using current landscape and ecosystem-level parameters, using a point range of 0 to 100, with higher values denoting a higher level of endangerment. The point thresholds for different categories of conservation status were as follows: critical 89–100 points, endangered 65–88, vulnerable 37–64, relatively stable 7–37, and relatively intact 0–6. Total point values were determined by summing points assigned for each parameter. Individual parameter point values were associated with different landscape scenarios. For example, total habitat loss scenarios were related to points as follows:

% Original habitat	Heavily altered	Altered
90–100%	40	20
75–89%	30	15
50–74%	20	10
10–49%	10	5
0–9%	0	0

An ecoregion receives both a heavily altered score and an altered habitat score, which represents the amount of habitat in each category. For example, consider an ecoregion with 35% heavily altered habitat (10 points), 55% altered habitat (10 points), and therefore 10% intact habitat. By combining the two scores, the ecoregion would receive a total score of 20 points. Different quantitative and qualitative biodiversity and landscape ecology characteristics are used to define intact, altered, and heavily altered states tailored to the specific patterns and dynamics of different biomes. Total scores for each of the parameters are summed to give a total conservation status index score.

Snapshot scores were subsequently modified by a 20-year projected threat analysis to arrive at a final conservation status assessment. Ecoregions that were assessed as facing high threat were elevated to a more serious conservation status. The threat analysis estimated the cumulative impacts of all current and projected threats on habitat conversion, habitat degradation, and wildlife exploitation using a point system associated with different qualitative and quantitative impacts. Using an index of 0–100 points, pending threats within an ecoregion were assessed and point totals assigned for each of the above categories. Conversion threats were considered to be the most serious, and thus habitat loss comprised half (50) of all possible points in the weighting of threats. For example, 50 points were assigned to conversion threats if 25% or more of remaining habitat would be categorized as heavily altered within 20 years. For conversion of between 10% and 24% of remaining habitat, a score of 20 points was assigned. The remaining two threats, habitat degradation and wildlife exploitation, were assessed using maximum point totals of 30 and 20 respectively using a scale based on high, medium, or no threat.

EL GÉNERO *JUSTICIA* (ACANTHACEAE) EN SUDAMÉRICA AUSTRAL[1]

Cecilia Ezcurra[2]

Resumen

El género *Justicia* es el más grande y complejo de la familia Acanthaceae, y está muy diversificado en las regiones tropicales y subtropicales de América del Sur. Este trabajo comprende la revisión de las especies de Sudamérica austral sobre la base de material de Argentina y Paraguay. Las 38 especies de *Justicia* de esta región se agrupan en 8 secciones en relación a caracteres de su morfología, especialmente de inflorescencia, flor, cápsula y semilla. Todas las especies se describen, se dan referencias de ilustraciones ya publicadas o se ilustran por primera vez, y se da una clave para identificarlas. Algunas no habían sido citadas para la región, y la nomenclatura de las mismas incluye varias sinonimias nuevas basadas en el estudio de los tipos nomenclaturales. También se dan notas sobre su fenología, hábitat, distribución geográfica, caracteres distintivos y afinidades taxonómicas.

Abstract

The genus *Justicia* is the largest and most complex of the Acanthaceae family, and is highly diversified in tropical and subtropical regions of South America. This work revises the species of southern South America based on material from Argentina and Paraguay. The 38 species of *Justicia* that are found in this region are grouped in 8 sections in relation to their morphological characters, especially inflorescence, flower, capsule, and seed morphology. All the species are described, references to published illustrations are given or they are illustrated for the first time, and a key is provided for their identification. Some had not been reported previously for the region, and their nomenclature includes several new synonymies based on the study of type material. Notes on phenology, habitat, geographic distribution, distinguishing characters, and taxonomic affinities are also given.

Key words: Acanthaceae, *Justicia*, morphology, taxonomy, southern South America.

El género *Justicia* L. es el más grande y complejo de las Acantáceas a nivel mundial, y el de mayor número de especies en los regiones tropicales y subtropicales del continente americano. Este género comprende aproximadamente 600 especies de hierbas y arbustos perennifolios (Graham, 1988), varias de ellas importantes como forrajeras (Burkart, 1943) u ornamentales (Bailey, 1949; Parodi & Dimitri, 1980). Muchas de sus especies también tienen importancia ecológica por ser elementos abundantes en el sotobosque de selvas y bosques húmedos, o por ser frecuentes o dominantes en ambientes semiáridos. En México está representado por alrededor de 75 especies (Daniel,

[1] Agradezco a Tom Daniel por haberme cedido generosamente el estudio de las Acantáceas de Paraguay que originalmente pensaba realizar él. Mi reconocimiento a Ángel L. Cabrera por sugerirme este tema hace varios años, a Vladimiro Dudas por las ilustraciones, a Ana Ladio y Victoria Amos por la asistencia en la edición de las listas de ejemplares e índices, y a los curadores y personal de los siguientes herbarios por facilitar material para este estudio: BM, CORD, CTES, E, FCQ, G, K, LIL, LP, M, P, NY, MO, SI, US, W. También agradezco a Fátima Mereles, Isabel Basualdo, Rosa Degen y Nélida Soria su valiosa ayuda en Paraguay, tanto en el herbario (FCQ) como en el campo, y a Carlos Saravia Toledo su invalorable colaboración en viajes de colección y sus interesantes datos sobre distribución y ecología de las Acantáceas del Chaco.

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1993), en Colombia por 85 (Leonard, 1951–1958), en Ecuador por 27 (Jörgensen & León-Yánez, 1999), en Perú por 50 (Brako & Zarucchi, 1993), y en Argentina por 28 (Ezcurra, 1993a, 1999).

Hasta ahora no existen trabajos sobre la sistemática de este género en la porción austral de América del Sur, excepto algunos tratamientos regionales (Lindau, 1894, para Argentina; Rambo, 1964, para Río Grande do Sul, Brasil; Dawson, 1965 y 1979, para Buenos Aires y Entre Ríos, Argentina; Wasshausen & Smith, 1969, para Santa Catarina, Brasil; Ariza-Espinar, 1971, para el centro de Argentina; Ezcurra, 1993a, para Jujuy, Argentina). Debido a esto se propuso realizar un estudio de las especies de Argentina y Paraguay, países donde el género está especialmente representado y presenta una diversidad importante.

El objetivo principal de este trabajo es describir la morfología y resolver la nomenclatura de las especies de Sudamérica austral, lo que facilitará la identificación de la mayoría de las especies de la región subtropical y templada de América del Sur. Además este estudio comprende un análisis morfológico teniendo en cuenta especialmente la arquitectura de la inflorescencia, la morfología de la corola, y la forma y superficie de la semilla, caracteres que ya han sido señalados como importantes en la delimitación de grupos de especies afines dentro de *Justicia* (Ariza-Espinar, 1971; Graham, 1988; Lester & Ezcurra, 1991).

Historia Taxonómica y Delimitación del Género

El género *Justicia* fue propuesto por Linné en 1753. Un siglo después Nees, en su tratamiento de las Acantáceas a nivel mundial (1847b), redelimitó el género excluyendo más de 600 especies que se habían descripto bajo el nombre de *Justicia*, reduciéndolo a solo 12 especies de Asia y África. Por otro lado creó varios géneros nuevos afines a *Justicia* para ubicar un gran número de especies del Nuevo Mundo recientemente descubiertas. Bentham (1876) y Lindau (1895) ampliaron el concepto de *Justicia* de Nees y redujeron a la sinonimia muchos de los géneros creados por este último autor. Durante este siglo, los estudios taxonómicos de *Justicia* han seguido estas dos tendencias opuestas a través del tiempo, ya sea reconociendo un número grande de géneros afines a *Justicia* s. str. (por ej., Rizzini, 1949, 1951; Bremekamp, 1969), o adoptando una definición amplia que incluye a la mayoría de éstos como sinónimos (por ej., Leonard, 1951–1958). El problema de los límites del género ha sido discutido ampliamente en épocas recientes (por ej., Gibson, 1972; McDade, 1982; Ezcurra, 1988; Graham, 1988).

Actualmente la mayoría de los autores tratan a *Justicia* en su sentido más amplio siguiendo la propuesta de Graham (1988) (por ej., Wasshausen, 1992; Profice, 1993; Daniel, 1995; Kameyama, 1995). Este concepto amplio ha resultado en estimaciones de 600–700 especies para todo el género en los últimos años (Graham, 1988; McDade & Daniel, 1998). Sin embargo, no se sabe si la gran heterogeneidad de números cromosómicos que han sido citados para el género (Daniel, 2000) estarían reflejando evolución diversificadora a nivel cromosómico, o características polifiléticas del mismo (Daniel, 1993; Daniel et al., 1984; Piovano & Bernardello, 1991). Análisis moleculares preliminares (McDade & Daniel, 1998) indicarían que *Justicia* s. lat. conforma un linaje separado del resto de la tribu Justicieae, y que la gran diversificación morfológica y la alta tasa de especiación en este género se ha dado concomitantemente con muy poco cambio a nivel molecular en los loci analizados hasta el momento, lo que apoyaría la primera hipótesis. Actualmente se está trabajando para dilucidar las relaciones filogenéticas entre los taxa afines y pertenecientes a *Justicia* utilizando caracteres moleculares, morfológicos y cromosómicos, y un número mayor de representantes especialmente del Viejo Mundo (McDade et al., 2000).

Siguiendo el concepto de Graham (1988) el género *Justicia* comprende especies caracterizadas por corolas bilabiadas con surco estilar en la parte posterior interna, presencia de 2 estambres exsertos bajo el labio posterior, con 2 (raro 1) tecas, ausencia de estaminodios, polen subprolado a perprolado 2- o 3(4)-porado o colporado, y cápsulas 4-seminadas. Este criterio de delimitación del género es el que se sigue en este trabajo.

Materiales y Métodos

El estudio se realizó sobre la base de material de los principales herbarios de Paraguay y Argentina, y de varios herbarios extranjeros (BM, CORD, CTES, E, FCQ, G, K, LIL, LP, M, MO, NY, P, SI, US, W (abreviaturas según Holmgren et al., 1990); Apéndices 1, 2). Los ejemplares citados se seleccionaron como para ser representativos de la distribución y diversidad de cada especie en la región. La identificación de las especies se hizo por comparación con material tipo o fotografías del mismo, lo mismo que la resolución de los sinónimos nomenclaturales. Las fotografías de ejemplares tipo de la colección del Field Museum de Chicago, se designan con la abreviatura "fot. F" y el número

de la colección fotográfica. Este estudio incluyó la revisión de más de 220 ejemplares tipo.

En la mayoría de los casos de nombres creados por Nees (1847a, 1847b), este autor no designó holotipo sino que citó varios ejemplares representativos que deben considerarse sintipos. Debido a que no pude consultar todos los sintipos de cada nombre por estar estos ejemplares distribuidos en varios herbarios europeos, en este trabajo generalmente no designé lectotipos de entre estos sintipos. Nees (1847a, 1847b) tampoco designó claramente una variedad tipo cuando estableció varios taxa infraespecíficos para una especie, sino que las designó con letras del alfabeto griego. Por las razones ya expuestas previamente (Ezcurra, 1993c), considero en esos casos a la variedad alfa como la variedad tipo de cada especie. En los casos en que este autor no designara una variedad alfa pero describiera variedades con letras subsecuentes (beta, gama, etc.), considero a la descripta en la descripción general de la especie como la variedad tipo.

Otro problema que surgió en cuanto a la tipificación se relaciona con los ejemplares de Sellow. Muchas de las especies descriptas por Nees (1847a, 1847b) que se tratan en este trabajo fueron descriptas sobre la base de material de Sellow del sur de Brasil que estaba depositado en el herbario de Berlín que fue destruido durante la segunda guerra mundial. Existen duplicados de varios de estos ejemplares en Kew, los que se reconocen por los datos "Herb. Reg. Berolinense, Brasilia, Sellow legit." que figuran en las etiquetas. Como en general estos son los únicos datos que figuran en sus etiquetas (falta información sobre la localidad y número de colección), no se puede saber con seguridad si realmente son duplicados de los holotipos que estaban en Berlín que utilizó Nees para sus descripciones. Pero cuando en estos ejemplares figura el nombre de la especie manuscrito por Nees, considero que muy posiblemente sean duplicados del mismo material que Nees vio en Berlín, y en este trabajo los cito como "probables" isotipos o isosintipos.

El estudio de la distribución geográfica y de los requerimientos ecológicos de las especies se hizo sobre la base de datos del material de herbario complementados con observaciones a campo de la mayoría de las especies tratadas. La cita de una especie para otros países siempre implica que he visto material de esos países.

Los caracteres morfológicos se analizaron en forma comparada en todas las especies presentes en el área, agrupándose las mismas mediante búsqueda de correlaciones que considero señalan posibles afinidades filogenéticas. Muchas de las especies del área en estudio eran muy poco conocidas y no habían sido tenidas en cuenta al elaborar el sistema de clasificación vigente (Graham, 1988).

Morfología

La diversidad morfológica del género ha sido tratada por Graham (1988). Aquí se discuten principalmente los caracteres con valor taxonómico para diferenciar las especies presentes en Argentina y Paraguay, y se realizan observaciones en especial sobre las especies que no fueron incluidas en el trabajo de Graham (1988) para ubicarlas dentro del esquema de clasificación de esta autora (Tabla 1).

Arquitectura de la inflorescencia. Los tipos de inflorescencia de las Acantáceas en general, incluyendo varias especies de *Justicia*, han sido tratados en detalle por Sell (1969, 1976). Graham (1988) utiliza un sistema más simple de clasificación de inflorescencias, que es el que se sigue en este trabajo. Las especies de Sudamérica austral, coincidiendo en general con las del Nuevo Mundo (Graham, 1988) poseen (1) inflorescencias compuestas (espigas de espigas, o panojas de espigas) (dibotrioides o tribotrioides según Sell, 1969), como en *J. corumbensis*, *J. jujuyensis*, *J. oblonga*, *J. oranensis* y *J. saltensis*, o (2) inflorescencias simples (espigas simples) (monobotrioides según Sell, 1969), como en *J. axillaris*, *J. chacoënsis*, *J. cuspidulata*, *J. gilliesii*, *J. hunzikeri*, *J. lilloana*, *J. phyllocalyx* y algunas formas de *J. pectoralis* y *J. saltensis*, o (3) flores solitarias, como en *J. riojana* y *J. tweediana* y en algunas formas de *J. axillaris*. Las espigas de *Justicia* muchas veces son secundifloras, como en *J. glaziorii*, *J. goudotii*, *J. laevilinguis* y *J. saltensis*. A veces en una especie se combinan inflorescencia simples y compuestas, como las espigas y racimos de espigas que se encuentran en *J. saltensis* y *J. xylosteides*. Las flores solitarias y las inflorescencias simples probablemente deriven de inflorescencias compuestas (Sell, 1976). Además de este tipo de condensación, en la evolución del género también pudo haber habido elaboración de inflorescencias simples a compuestas por combinación de espigas axilares con espigas terminales (Graham, 1988).

Morfología de la corola. Las corolas de *Justicia* son marcadamente cigomorfas. Típicamente están compuestas por un tubo basal cilíndrico, una garganta más o menos tubulosa o campanulada apicalmente dividida en dos labios, un labio superior angosto, erecto, más o menos convexo y bidentado, y un labio inferior ancho, más o menos patente y trilobado. En las especies de Sudamérica austral

Table 1. Especies de *Justicia* presentes en Sudamérica austral, sección a la que pertenecen, probable tipo de polinización, clase de ornamentación de la superficie seminal (Graham, 1988: A, tuberculada, verrugosa o pusticulada; B, pilosa o papiloso-pilosa; C, lisa a muy levemente rugosa), y provincia fitogeográfica en la que se encuentran. (Con asterisco* las especies que no habian sido classificadas por Graham, 1988, con signo de pregunta ? las que no se conoce su semilla madura).

Especie	Sección	Polinización	Semilla	Fitogeogr.
1. *Justicia aequilabris*	*Orthotactus*	Ornitofilia	A	Cerrado
2. *Justicia axillaris**	*Dianthera* subsect. *Saglorithys*	Melitofilia	A	Paranaense
3. *Justicia baenitzii*	Incierta	Ornitofilia	?	Yungas
4. *Justicia brasiliana*	*Plagiacanthus*	Ornitofilia	C	Paranaense
5. *Justicia carnea*	*Cyrthanthera*	Ornitofilia	?	Paranaense
6. *Justicia chacoënsis**	*Orthotactus*	Ornitofilia	A	Chaqueña
7. *Justicia comata*	Incierta	Melitofilia	A	Chaqueña
8. *Justicia corumbensis**	*Plagiacanthus*	Melitofilia	C	Chaqueña
9. *Justicia cuspidulata**	*Dianthera* subsect. *Saglorithys*	Melitofilia	A	Cerrado
10. *Justicia dumetorum*	*Simonisia*	Ornitofilia	C	Chaqueña
11. *Justicia floribunda*	*Plagiacanthus*	Ornitofilia	C	Paranaense
12. *Justicia gilliesii**	*Sarotheca*	Melitofilia	A	Chaqueña
13. *Justicia glaziovii*	*Sarotheca*	Melitofilia	A	Cerrado
14. *Justicia glutinosa*	*Sarotheca*	Melitofilia	A	Chaqueña
15. *Justicia goudotii*	*Chaetothylax*	Lepidopterofilia	B	Chaqueña
16. *Justicia hassleri*	*Leucoloma*	Lepidopterofilia	B	Paranaense
17. *Justicia hunzikeri**	*Orthotatus*	Melitofilia	A	Chaqueña
18. *Justicia jujuyensis**	*Plagiacanthus*	Melitofilia	C	Yungas
19. *Justicia kuntzei*	*Sarotheca*	Melitofilia	A	Yungas
20. *Justicia laevilinguis*	*Dianthera* subsect. *Dianthera*	Melitofilia	C	Paranaense
21. *Justicia lilloana**	Incierta	Melitofilia	C	Chaqueña
22. *Justicia lilloi*	*Simonisia*	Melitofilia	C	Chaqueña
23. *Justicia lythroides*	*Chaetothylax*	Melitofilia	B	Paranaense
24. *Justicia mandoni*	*Simonisia*	Ornitofilia	A	Yungas
25. *Justicia oblonga**	*Chaetothylax*	Melitofilia	B	Paranaense
26. *Justicia oranensis**	*Sarotheca*	Ornitofilia	A	Yungas
27. *Justicia pectoralis*	*Sarotheca*	Melitofilia	A	Chaqueña
28. *Justicia phyllocalyx**	*Simonisia*	Melitofilia	?	Cerrado
29. *Justicia polygaloides*	*Dianthera* subsect. *Saglorithys*	Melitofilia	A	Paranaense
30. *Justicia ramulosa*	*Chaetothylax*	Ornitofilia	B	Paranaense
31. *Justicia riojana**	*Plagiacanthus*	Melitofilia	C	Chaqueña
32. *Justicia rusbyi*	*Simonisia*	Melitofilia	C	Cerr. y Par.
33. *Justicia saltensis**	*Sarotheca*	Melitofilia	B	Chaqueña
34. *Justicia squarrosa*	*Simonisia*	Lepidopterofilia	C	Chaqueña
35. *Justicia tocantina*	*Chaetothylax*	Ornitofilia	B	Chaqueña
36. *Justicia tweediana*	*Plagiacanthus*	Melitofilia	C	Chaqueña
37. *Justicia xylosteoides**	*Orthotactus*	Ornitofilia	A	Chaqueña
38. *Justicia yhuensis*	*Dianthera* subsect. *Strobiloglossa*	Melitofilia	B	Cerrado

esta estructura básica está ampliamente diversificada, probablemente en respuesta a la presión selectiva de diferentes tipos de polinizadores durante la evolución del género. Esta gran diversidad morfológica de las corolas, similar a la descripta para las especies de *Ruellia* de Sudamérica austral (Ezcurra, 1993c), comprende principalmente tres tipos (Fig. 1, Tabla 1).

El primer tipo se caracteriza por las corolas de color blanco o lila con el tubo, garganta y labios proporcionalmente cortos y anchos, generalmente con manchas y marcas venosas en la fauce, probablemente polinizadas por insectos del grupo de las abejas (flores melitófilas, Fig. 1A, B). Este es el grupo más numeroso en Sudamérica austral y es muy variable en tamaño, ya que existen especies con flores de este tipo de unos pocos mm de longitud (por ej., *Justicia comata*, *J. glaziovii*, *J. polygaloides*) hasta de varios centímetros de longitud (por ej., *Justicia lilloi*, *J. rusbyi*).

El segundo tipo se caracteriza por las corolas de color rosa, rojo o morado, grandes, con el tubo, gar-

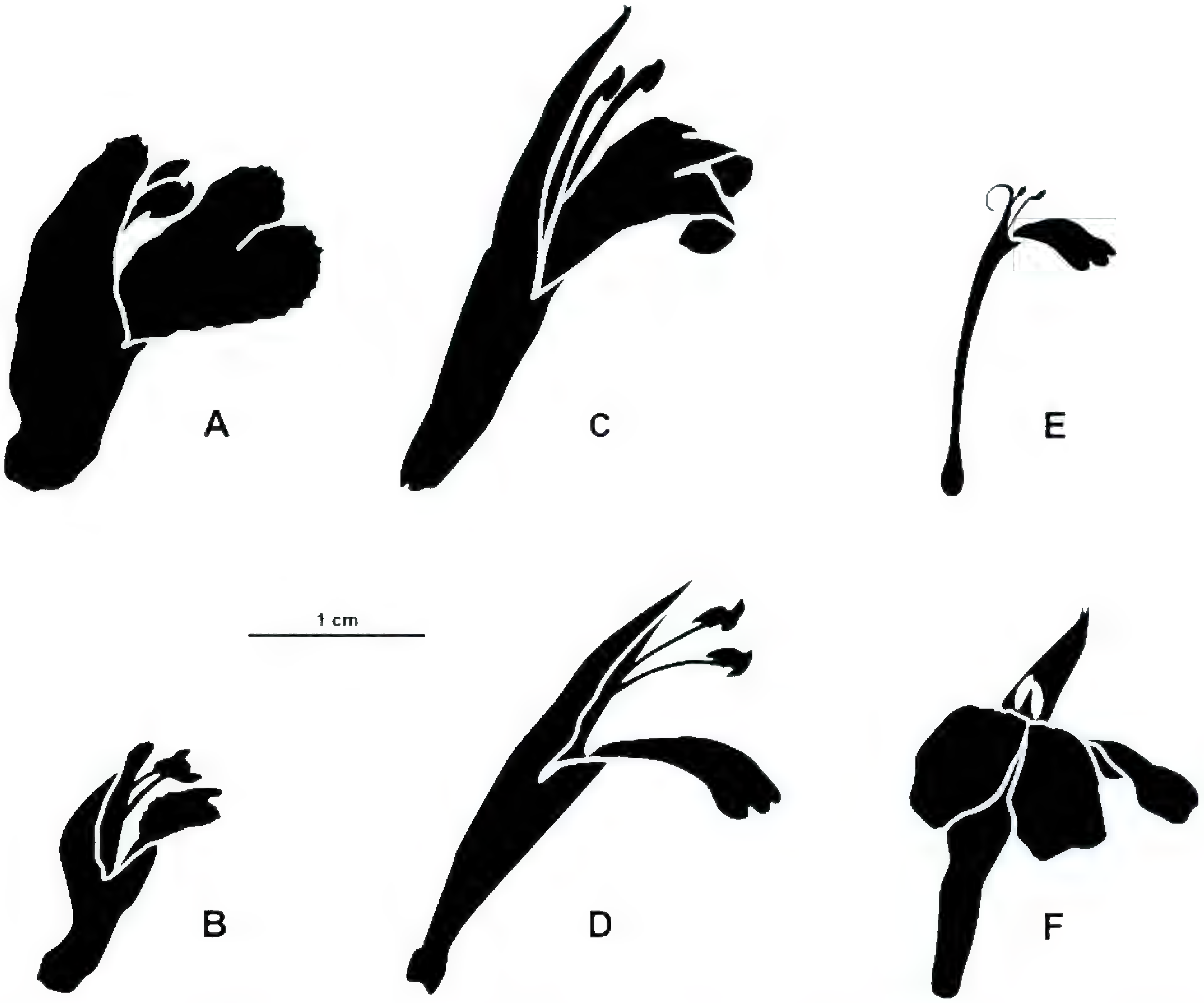

Figura 1. Tipos de corolas de las especies de *Justicia* presentes en Sudamérica austral. A, B. Corolas melitófilas. —A. *J. tweediana.* —B. *J. jujuyensis.* C, D. Corolas ornitófilas. —C. *J. mandoni.* —D. *J. oranensis.* E, F. Corolas lepidopterófilas: —E. *J. goudotii.* —F. *J. squarrosa.* (Esquematizadas a partir de ilustraciones de Ezcurra, 1993a.)

ganta y labios proporcionalmente angostos y largos, aparentemente adaptadas a la polinización por picaflores (flores ornitófilas, Fig. 1C, D). En general este tipo de corola mide de 2.5–5 cm de longitud, y también está muy representado en la región (por ej., *Justicia baenitzii, J. brasiliana, J. dumetorum, J. floribunda, J. mandoni, J. ramulosa, J. xylosteoides*), lo que se relaciona con la importancia de la polinización por picaflores en América del Sur tropical y subtropical (Gentry, 1982).

Un tercer tipo se caracteriza por las corolas de color rosado, lilacino o blanco, con el tubo y garganta muy estrechos y el labio anterior extendido, aparentemente adaptadas a polinización por mariposas (flores lepidopterófilas, Fig. 1E, F) (por ej., *Justicia goudotii* y *J. squarrosa* de flores lilacinas, y *J. hassleri* de flores blancas).

Muchas veces los distintos tipos de flores están representados dentro de una misma sección de *Justicia.* Esto sugiere que, al igual que en *Ruellia* (Ezcurra, 1993c), la morfología de la corola de *Justicia* ha resultado un carácter evolutivamente muy plástico ante la presión selectiva de diferentes tipos de polinizadores. De esta manera la forma de la flor parece haberse diversificado mucho en el grupo, incluso dentro de diferentes linajes, diferenciándose entre especies muy relacionadas en otros aspectos (como por ejemplo la ornitófila *J. ramulosa* y la psicófila *J. goudotii* de la sect. *Chaetothylax*), lo que hace que en general sea un carácter poco importante en la delimitación de grupos de especies relacionadas.

Morfología del polen. La llamativa diversidad del polen de las Acantáceas en general y de *Justicia* en particular ha sido descripto por Lindau (1893, 1895), Raj (1961, 1973), Petriella (1968), Graham (1988), y Daniel (1998). *Justicia* se caracteriza típicamente por el polen 2(–4) porado o 2(–4) colporado, prolado, dorsiventralmente aplanado cuando biaperturado, con el mesocolpio reticuladamente esculturado, y la apertura con 1–3 hileras

de ínsulas o esculturas sexinosas a cada lado del poro. Sin embargo, existen muchas variaciones de este esquema dentro del género (Graham, 1988). Parte de la diversidad morfológica del polen de las especies de *Justicia* del sur de Sudamérica se describe en Petriella (1968) y Wasshausen y Ezcurra (1997). *Justicia phyllocalyx* se diferencia marcadamente del resto del género por presentar toda la superficie cubierta de ínsulas ordenadas en líneas sub-paralelas al eje longitudinal (Wasshausen & Ezcurra, 1997). La cobertura de ínsulas hace que se asemeje a especies del género *Poikilacanthus*, un género muy afín a *Justicia* cuyas estrechas relaciones deberían estudiarse (Daniel, 1998).

Forma y superficie de la semilla. Como fue sugerido por Ariza-Espinar (1971), ciertos caracteres de la morfología de las semillas han resultado muy útiles para el reconocimiento de taxones infragenérica en *Justicia*, en especial el grado de compresión, el margen, y la superficie (Graham, 1988; Lester & Ezcurra, 1991). Recientemente se ha publicado un estudio con microscopio electrónico de barrido de semillas de doce especies de Argentina (Peixoto, 1998). En el presente trabajo se presentan microfotografías con MEB de otras nueve especies del sur de Sudamérica (Figs. 2–4) que no fueron tratadas por Peixoto (1998), y se dan las características macromorfológicas de las semillas de todas las especies en las descripciones generales. Estas características han sido utilizadas para clasificar o confirmar la clasificación infragenérica previa de las especies aquí tratadas (Tabla 1). La morfología de las semillas coincide con la descripta por Graham (1988) para las secciones en las que se ubican las especies.

Las especies de Sudamérica austral poseen en su mayoría semillas comprimidas, más o menos biconvexas y lenticulares, como *J. cuspidulata* (Fig. 2C), *J. hassleri* (Fig. 2E), *J. lythroides* (Fig. 3C), *J. pectoralis* (Fig. 3E), *J. saltensis* (Fig. 4C) y *J. xyloestoides* (Fig. 4E). Algunas semillas comprimidas son plano-convexas y tienen un reborde grueso en el margen del lado plano, como *J. corumbensis* (Fig. 2A), *J. brasiliana*, y *J. jujuyensis* de la sección *Plagiacanthus*. Una minoría de las especies de esta región presentan semillas esféricas, como *J. lilloi* (Fig. 3A), *J. rusbyi* (Fig. 4A), *J. phyllocalyx* y *J. squarrosa*, pertenecientes a la sección *Simonisia*.

La superficie en general varía entre las tres clases principales descriptas por Graham (1988) para el género: (A) rugulosa, pusticulada, verrugosa o tuberculada, (B) pubescente (pilosa o papiloso-pilosa), y (C) más o menos lisa (Tabla 1). Ejemplos de superficie verrugosa a tuberculada (A) se encuentran en *J. cuspidulata* (Fig. 2D) y *J. axillaris* y de la sect. *Dianthera* subsect. *Saglorithis*, *J. xylosteoides* (Fig. 4F) de la sect. *Orthotactus*, y *J. comata* de posición incierta. Ejemplos de superficie pubescente (B) con pelos cortos aparecen en *J. hassleri* (Fig. 2F) de la sect. *Leucoloma*, con pelos más o menos gloquidiados en *J. lythroides* (Fig. 3D), *J. oblonga* y demás especies de la sect. *Chaetothylax*, y con pelos levemente capitados en *J. pectoralis* (Fig. 3F). En *J. saltensis* (Fig. 4D) de la sect. *Sarotheca* los pelos son capitados y gloquidiados. Superficies lisas (C) aparecen en *J. laevilinguis* de la sect. *Dianthera* subsect. *Dianthera* y *J. lilloana* de posición incierta, más o menos lisa en las especies de la sect. *Plagiacanthus* como *J. corumbensis* (Fig. 2B), y lisa y lustrosa en las especies de la sect. *Simonisia*, como *J. lilloi* (Fig. 3B) y *J. rusbyi* (Fig. 4B).

Cromosomas. Se han estudiado los cromosomas de varias especies de *Justicia* (Grant, 1955; Piovano & Bernardello, 1991; Daniel et al., 1984, 1990; Daniel & Chuang, 1993; Daniel, 2000). El número básico del género parece ser $x = 7$ y el número más común $n = 14$. Sin embargo, no está claro si la gran diversidad de los números ($n = 7$, 9–18, 20, 22–25, 27–29, 31 y 34) encontrados en *Justicia* s.l. sugiere una evolución diversificadora o un origen polifilético del género (Daniel et al., 1984). Aunque se han encontrado algunas coincidencias preliminares entre la clasificación infragenérica en secciones de Graham (1988) y los números cromosómicos de las especies, está claro que *Justicia* necesita todavía más estudio a nivel cromosómico (Daniel, 2000). Los pocos recuentos publicados de especies de Argentina y Paraguay han dado $n = 14$ o $2n = 28$ (*J. brasiliana*, *J. gilliesii*, *J. oranensis*, *J. squarrosa* y *J. tweediana*) excepto en *J. xylosteoides*, $2n = 32$ (Piovano & Bernardello, 1991).

Distribución geográfica. *Justicia* es un género muy diversificado en sus requerimientos ecológicos. En Paraguay está representado en todos los ambientes de las provincias fitogeográficas en que se divide el país: del Cerrado, Paranaense y Chaqueña, y en Argentina también se encuentra en las provincias de las Yungas, de la Prepuna, del Monte, del Espinal y Pampeana (Cabrera & Willink, 1980) (Tabla 1).

Especies xerófilas típicas de la provincia Chaqueña son, por ej., *Justicia squarrosa* y *J. xylosteoides*, que aparecen exclusivamente en ambientes semiáridos de la porción occidental de la región, mientras que especies hidrófilas típicas de la provincia Paranaense son, por ej., *J. brasiliana* y *J.*

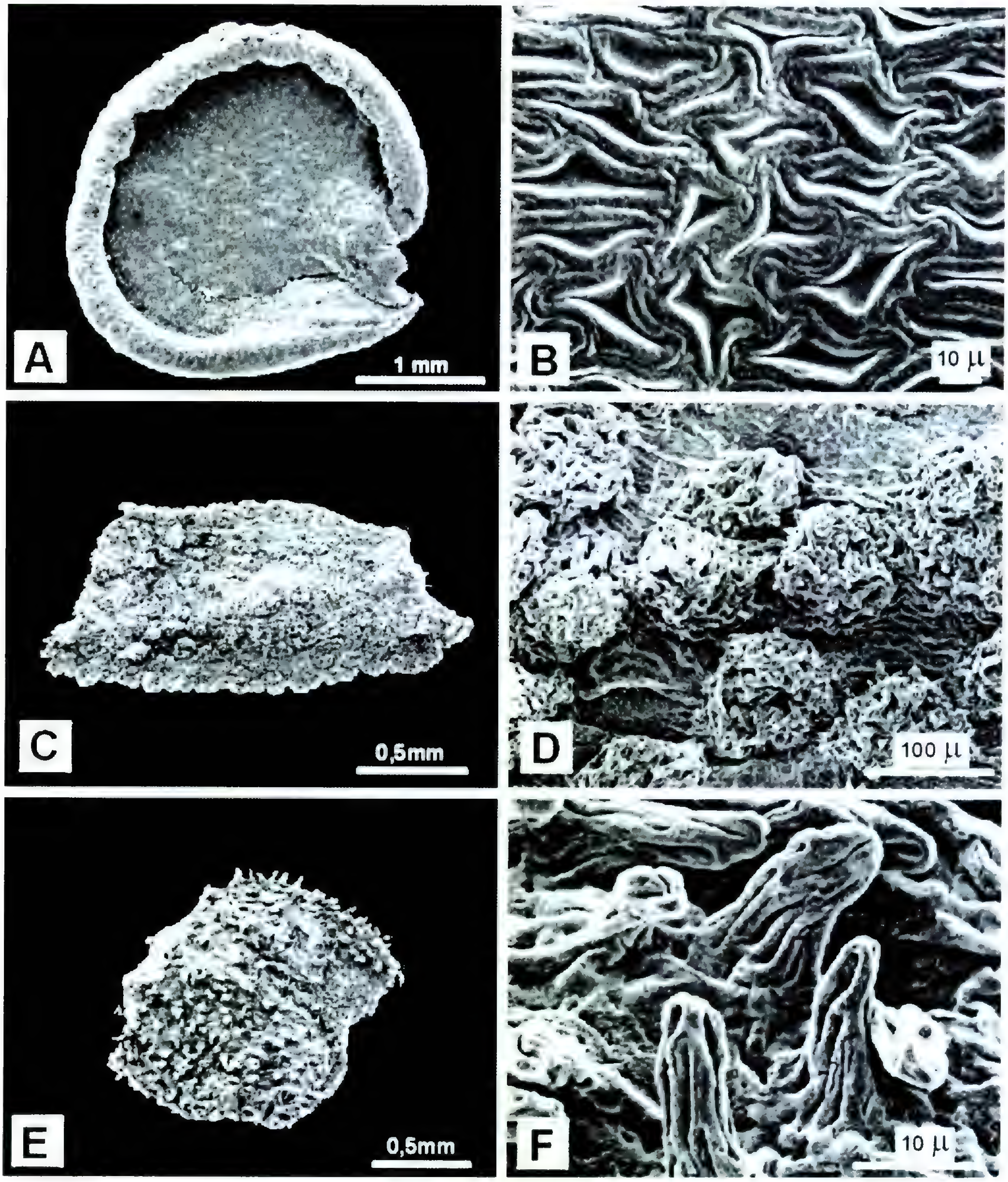

Figura 2. Tipos de semillas de las especies de *Justicia* presentes en Sudamérica austral. A, B. *J. corumbensis* (*Bernardi 20142*). —A. Aspecto general de la cara cóncava con reborde. —B. Detalle de la superficie lisa. C, D. *J. cuspidulata* (*Schinini y Bordas 20534*). —C. Aspecto general. —D. Detalle de la superficie verrugosa. E, F. *J. hassleri* (*Zardini y Velázquez 9943*). —E. Aspecto general. —F. Detalle de la superficie cortamente verrugoso-pilosa.

carnea, que solamente se encuentran en bosques húmedos del noreste de Argentina y Paraguay oriental. Existe un pequeño grupo de especies de *Justicia* endémicas de Sudamérica austral (*J. gilliesii*, *J. hunzikeri*, *J. riojana*, *J. lilloana*), aunque la mayoría en general tienen una distribución que excede los límites de la región. Muchas además son características de condiciones locales y edáficas particulares, como las especies de ambientes anegados (por ej., *J. laevilinguis*), o de campos abiertos y arenosos sometidos a incendios periódicos (por ej., *J. axillaris*), o de bosques en galería de la región chaqueña (*J. corumbensis*).

No existe relación entre la taxonomía infragenérica y la distribución geográfica, ya que dentro de una misma sección puede haber especies de todos los ambientes. Aparentemente el área extensa y la diversidad de ambientes de la región subtropical y tropical de América del Sur habrían permitido la evolución y diversificación de varios li-

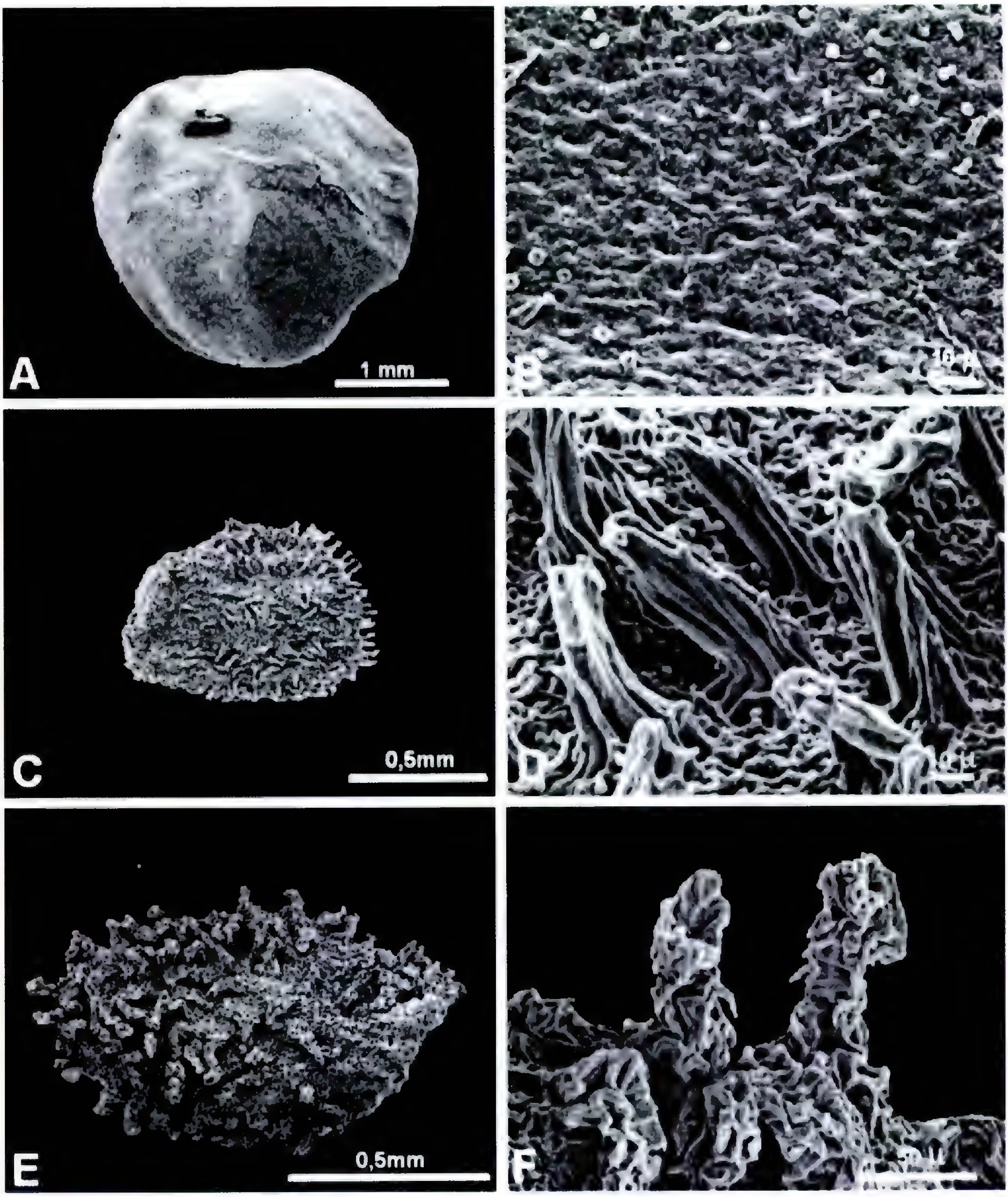

Figura 3. Tipos de semillas de las especies de *Justicia* presentes en Sudamérica austral. A, B, *J. lilloi* (*Mereles 2718*). —A. Aspecto general de la forma esférica. —B. Detalle de la superficie lisa. C, D, *J. lythroides* (*Degen 1522*). —C. Aspecto general. —D. Detalle de la superficie pilosa, con pelos gloquidiados. E, F, *J. pectoralis* (*Schinini y Palacios 25788*). —E. Aspecto general. —F. Detalle de la superficie pilosa, con pelos levemente capitados.

najes distintos de *Justicia*, muchos de ellos representados por las numerosas especies presentes en la gran heterogeneidad del territorio.

Taxonomía

El análisis morfológico permitió confirmar la posición taxonómica de varias de las especies presentes en la región, y proponer la ubicación de otras 14 (marcadas con asterisco en la tabla) que no habían sido tenidas en cuenta dentro del esquema clasificatorio propuesto por Graham (1988) (Tabla 1). El esquema clasificatorio de esta autora parece ser robusto, ya que permite acomodar estas especies.

En Sudamérica austral están representadas ocho de las nueve secciones del género que existen en el Nuevo Mundo: *Justicia* L. sect. *Chaetothylax* (Nees) V. A. W. Graham, sect. *Cyrtanthera* (Nees) V. A. W. Graham, sect. *Dianthera* (L.) V. A. W.

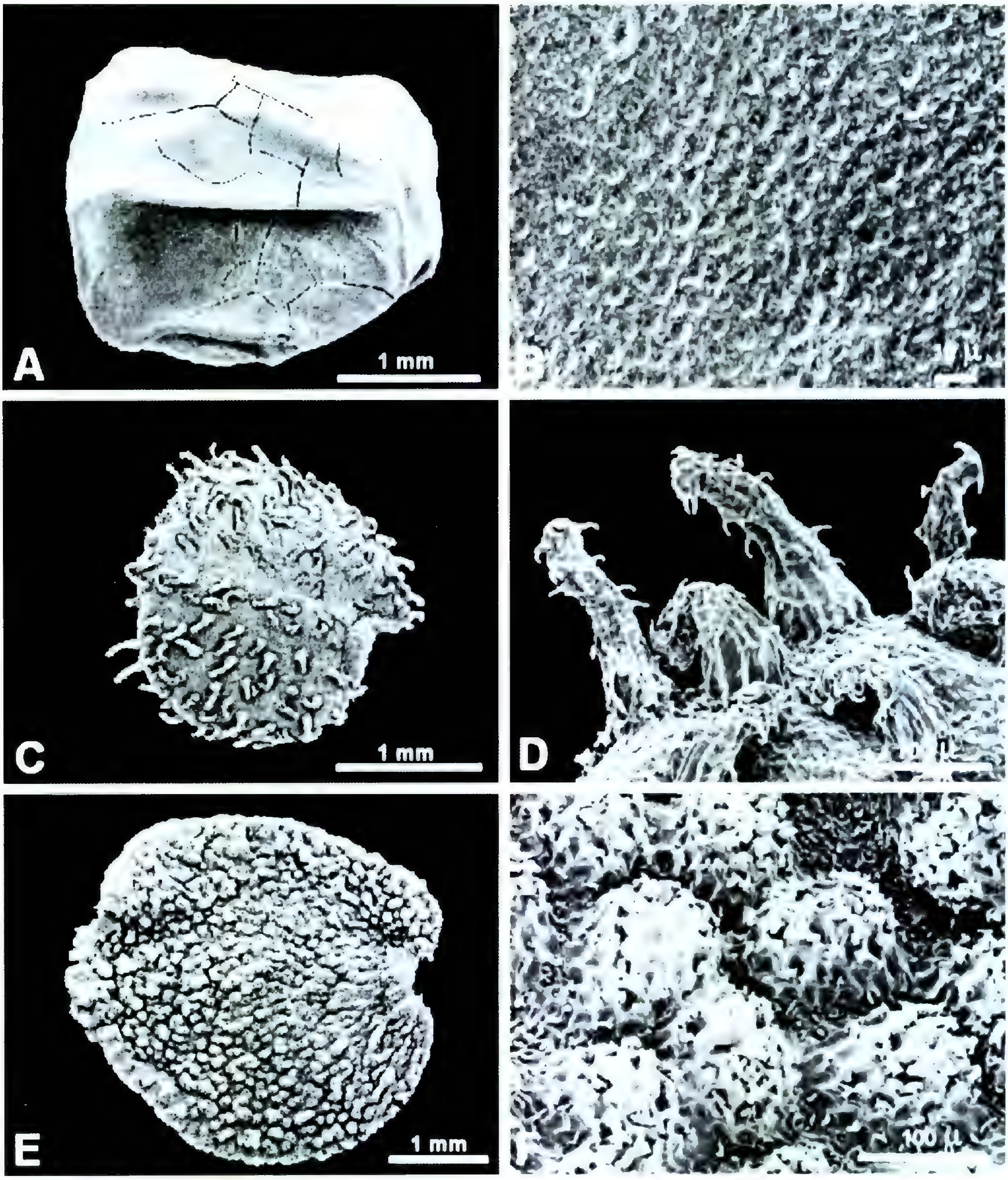

Figura 4. Tipos de semillas de las especies de *Justicia* presentes en Sudamérica austral. A, B, *J. rusbyi* (*Arbo 2664*). —A. Aspecto general de la forma esférica. —B. Detalle de la superficie lisa. C, D, *J. saltensis* (*Duré 428*). —C. Aspecto general. —D. Detalle de la superficie pilosa, con pelos capitados. E, F, *J. xylosteoides* (*Krapovickas y Cristóbal 14290*). —E. Aspecto general. —F. Detalle de la superficie verrugosa.

Graham subsect. *Dianthera*, sect. *Dianthera* (L.) V. A. W. Graham subsect. *Saglorithys* (Rizzini) V. A. W. Graham, sect. *Dianthera* (L.) V. A. W. Graham subsect. *Strobiloglossa* (Oersted) V. A. W. Graham, sect. *Leucoloma* V. A. W. Graham, sect. *Orthotactus* (Nees) V. A. W. Graham, sect. *Plagiacanthus* (Nees) V. A. W. Graham, sect. *Sarotheca* (Nees) Bentham, sect. *Simonisia* (Nees) V. A. W. Graham. El hecho de que la región subtropical de América del Sur sea un centro de diversidad tan importante para el género sugiere una larga historia evolutiva en la región y un posible origen sudamericano para el mismo.

La siguiente sinonimia incluye solamente los nombres genéricos que han sido utilizados para especies presentes en Sudamérica austral. Para una sinonimia más completa, véase Graham (1988) y Daniel (1995). En esta lista se da el nombre de la especie tipo de cada nombre genérico y su sinónimo en *Justicia*. Los sinónimos homotípicos se

marcan con el símbolo ≡, y los basados en tipos diferentes con el símbolo =. En Apéndice 3 se presenta un índice de nombres científicos y de nombres vulgares.

Justicia L., Sp. Pl. 1: 15. 1753, nom. cons. prop. TIPO: (lectotipo, designado por Hitchcock en Hitchcock & Green, 1930) *Justicia hyssopifolia* L.

Dianthera L., Sp. Pl. 1: 27. 1753. TIPO: *Dianthera americana* L. [≡ *Justicia americana* (L.) Vahl].
Adhatoda P. Miller, Gard. Dict. Abr. Ed. 4, 1. 1754. TIPO: *Adhatoda zeylanesium* Miller [= *Justicia adhatoda* L.].
Amphiscopia Nees, in Wall., Pl. Asiat. Rar. 3: 77, 112. 1832. TIPO: *Amphiscopia beyrichii* Nees.
Beloperone Nees, in Wall., Pl. Asiat. Rar. 3: 76. 1832. TIPO: (lectotipo, designado por Graham, 1988) *Beloperone amherstiae* Nees [= *Justicia brasiliana* Roth].
Leptostachya Nees, in Wall., Pl. Asiat. Rar. 3: 76, 105. 1832. TIPO: (lectotipo, designado por Graham, 1988) *Leptostachya virgata* [≡ *Justicia virgata* (Nees) T. Anders.].
Rhytiglossa Nees, in Lindl., Nat. Syst. Ed. 2, 444. 1836. TIPO: (lectotipo, designado por Wasshausen, 1966) *Rhytiglossa origanoides* Nees [≡ *Justicia origanoides* (Nees) Griseb., non Vahl].
Ethesia Raf., Fl. Tellur. 4: 63. 1838, non Raf. 1837. TIPO: *Ethesia carnea* (Lindl.) Raf. [≡ *Justicia carnea* Lindl.].
Stethoma Raf., Fl. Tellur. 4: 61. 1838. TIPO: *Stethoma pectoralis* (Jacq.) Raf. [≡ *Justicia pectoralis* Raf.].
Orthotactus Nees, in Martius, Fl. Bras. 9: 133. 1847. TIPO: (lectotipo, aquí designado) *Orthotactus venosus* Nees [≡ *Justicia aequilabris* (Nees) Lindau].
Heinzelia Nees, in Martius, Fl. Bras. 9: 153. 1847. TIPO: (lectotipo, designado por Graham, 1988) *Heinzelia lythroides* Nees [≡ *Justicia lythroides* (Nees) Graham].
Chaetothylax Nees, in Martius, Fl. Bras. 9: 153. 1847. TIPO: *Chaetothylax tocantinus* Nees [≡ *Justicia tocantina* (Nees) V. A. W. Graham].
Cyrtanthera Nees, in Martius, Fl. Bras. 9: 99. 1847. TIPO: (lectotipo, designado por Leonard, 1951–1958) *Cyrtanthera magnifica* Nees [= *Justicia carnea* Lindl.].
Sericographis Nees, in Martius, Fl. Bras. 9: 107. 1847. TIPO: (lectotipo, designado por Leonard, 1951–1958) *Sericographis rigida* Nees [≡ *Justicia sericographis* V. A. W. Graham].
Sarotheca Nees, in Martius, Fl. Bras. 9: 113. 1847. TIPO: (lectotipo, designado por Graham, 1988) *Sarotheca elegans* Nees [≡ *Justicia glutinosa* (Bremek.) V. A. W. Graham].
Jacobinia Nees, in Moric., Pl. Nouv. Amér.: 156. 1847. TIPO: *Jacobinia lepida* Nees [≡ *Justicia lepida* (Nees) Wassh.].
Ecbolium O. Kuntze, Rev. Gen. 2: 486. 1891, non S. Kurz 1871. Sinónimo nomenclatural de *Justicia* L. 1753 (por lectotipificación). TIPO: *Justicia hyssopifolia* L.
Chaetochlamys Lindau, Bull. Herb. Boiss. 3: 490. 1895. TIPO: (lectotipo, designado por Graham, 1988) *Chaetochlamys macrosiphon* Lindau [≡ *Justicia macrosiphon* (Lindau) V. A. W. Graham].
Cyphisia Rizzini, Rev. Brasil. Biol. 6: 521. 1946. TIPO: *Cyphisia venusta* Rizzini [≡ *Justicia venusta* (Rizzini) V. A. W. Graham].
Psacadocalymma Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 45: 55. 1948. TIPO: *Psacadocalymma comata* (L.) Bremek. [≡ *Justicia comata* L.].
Lophothecium Rizzini, Arch. Jard. Bot. Rio de Janeiro 8: 335. 1948. TIPO: *Lophotecium paniculatum* Rizzini [≡ *Justicia glaziovii* Lindau].
Acelica Rizzini, Arch. Jard. Bot. Rio de Janeiro 9: 55. 1949. TIPO: *Acelica cydoniifolia* (Nees) Rizzini basada en *Adhatoda cydoniifolia* Nees [≡ *Justicia cydoniifolia* (Nees) Lindau].
Pupilla Rizzini, Arch. Jard. Bot. Rio de Janeiro 9: 56. 1949. TIPO: *Pupilla heterophylla* (Nees) Rizzini basada en *Leptostachya heterophylla* Nees [≡ *Justicia heterophylla* (Nees) Lindau].
Thalestris Rizzini, Dusenia 3: 189. 1952. TIPO: *Thalestris graminiformis* Rizzini [≡ *Justicia comata* L.].

Hierbas perennes, sufrútices o arbustos erectos, procumbentes o ascendentes, glabros o pubescentes, con cistolitos. Hojas opuestas, sésiles o pecioladas, generalmente enteras, raramente crenadas o crenuladas. Inflorescencia terminal o axilar, las flores sésiles o cortamente pediceladas, con dos bractéolas, solitarias, fasciculadas o cimosas, en las axilas de brácteas, éstas frecuentemente dispuestas en espigas o tirsos, que a su vez a veces se agrupan en racimos o panojas; brácteas y bractéolas variadas. Cáliz profundamente 4- o 5-partido, los 4 o 5 segmentos generalmente angostos y subiguales. Corola marcadamente cigomorfa, roja, morada, lilacina o blanca, raras veces amarilla o naranja, el tubo más o menos angosto a campanulado, derecho o incurvado, con surco estilar en la parte posterior, a veces ampliado en la garganta y con marcas coloreadas en la fauce, del lado anterior, el limbo bilabiado, el labio posterior interno en la prefloración, generalmente angosto, erecto o incurvado, a veces cóncavo, con el ápice entero, bífido o levemente bilobado, y el labio anterior más ancho, más o menos patente o recurvado, profundamente a levemente trilobado. Estambres 2, los filamentos generalmente insertos abajo, cerca, o por encima de la mitad del tubo, filiformes o algo dilatados en la base; anteras exertas, bitecas, las tecas generalmente oblongas, a veces levemente curvadas o reniformes, discretas, superpuestas a cercanamente paralelas en el conectivo, a veces la inferior reducida, múticas, o una o ambas agudas, y apendiculadas o espolonadas en la base; estaminodios ausentes. Polen prolado, 2- o 3- o 4-porado o colporado, diversamente ornamentado, con la exina reticulada. Disco nectarífero anular, cupulado o ciatiforme, entero o sinuado-lobado. Estilo filifor-

me, exerto, diminutamente bilobado en el ápice. Óvulos 2 en cada lóculo. Cápsula de contorno oblongo, elíptico u obovado, con la porción basal sólida y lateralmente comprimida, y la porción superior cilíndrica, ovoide o subesférica, con los septos con retináculos. Semillas 4 o menos por aborto, generalmente comprimidas o lenticulares, a veces subglobosas, lisas o variadamente ornamentadas, rugosas, verrucosas o pilosas; retináculos curvos y agudos o truncados.

El genero *Justicia* comprende más de 600 especies ampliamente distribuidas en ambos hemisferios, especialmente en los trópicos, extendiéndose también a las regiones templadas del mundo. Presenta un centro de diversidad importante en Sudamérica, donde probablemente habiten cerca de 300 especies. Algunas de Sudamérica austral se cultivan como ornamentales por sus flores llamativas, como *Justicia carnea* (= *Jacobinia pohliana*, "vara de la justicia") y *Justicia floribunda* (= *Jacobinia pauciflora* o *Justicia rizzinii*, "banderita española") (Parodi & Dimitri, 1980), aunque existen varias otras nativas de Sudamérica austral con valor ornamental que merecerían cultivarse, como *J. oranensis* y *J. brasiliana*. Algunas también tienen importancia económica como forrajeras de emergencia, en épocas de escasez en gramíneas, como *Justicia tweediana* (= *J. campestris*, "alfalfilla") y *J. gilliesii* (= *J. echegarayi*, "albahaca de vaca") (Burkart, 1943).

Clave Artificial para las Especies de *Justicia* de Sudamérica Austral

1a. Flores de más de 2.5 cm long.
  2a. Flores lilacinas, azules y/o blancas.
    3a. Hojas axilantes de las flores o inflorescencias truncadas o cordadas .... *J. lilloi*
    3b. Hojas axilantes de las flores o inflorescencias obtusas a redondeadas .... *J. rusbyi*
  2b. Flores rosadas, rojas o moradas.
    4a. Flores en densos tirsos terminales; corolas de 5–6 cm long. .... *J. carnea*
    4b. Flores en inflorescencias variadas, nunca en tirsos densos; corolas menores.
      5a. Espigas con brácteas ovadas, elípticas u obovadas de más de 3 mm lat.
        6a. Brácteas de 7–9 mm lat.; cáliz 5-partido .... *J. aequilabris*
        6b. Brácteas de 3–5 mm lat.; cáliz 4 o 5-partido.
          7a. Cáliz 4-partido, flores rojo-moradas .... *J. ramulosa*
          7b. Cáliz 5-partido, flores rojo-anaranjadas .... *J. oranensis*
      5b. Espigas con brácteas más angostas.
        8a. Flores con corola angosta, de 2.5–3 cm long. por 2–4 mm diám.
          9a. Espigas densas; cáliz 4-partido .... *J. tocantina*
          9b. Espigas laxas; cáliz 5-partido .... *J. baenitzii*
        8b. Flores con corola más larga y ancha. Cáliz siempre 5-partido.
          10a. Espigas secundifloras.
            11a. Hojas subsésiles, de 0.7–1.5 cm lat.; arbustos xerófilos. Flores con labio posterior de 1–1.5 cm long. .... *J. xylosteoides*
            11b. Hojas pecioladas de 1.2–2.5 cm lat.; arbustos o subarbustos higrófilos. Flores con labio posterior de 1.5–2 cm long. .... *J. mandoni*
          10b. Espigas bilaterales o inflorescencias de otro tipo.
            12a. Flores solitarias o inflorescencias de espigas fasciculadas mucho más cortas que las hojas axilantes.
              13a. Inflorescencias axilares multifloras de flores rojas; brácteas espatuladas u oblanceoladas a lineales .... *J. brasiliana*
              13b. Espigas axilares paucifloras o unifloras de flores con el ápice amarillo; brácteas triangular-lanceoladas .... *J. floribunda*
            12b. Inflorescencias en espigas o racimos de espigas, más largas que las hojas axilantes.
              14a. Brácteas angostas, de ca. 1 mm lat., que ennegrecen al secarse. Flores rojas .... *J. chacoënsis*
              14b. Brácteas más anchas, de más de 2 mm lat., verdes, con el margen blanquecino y hialino. Flores moradas .... *J. dumetorum*
1b. Flores de menos de 2.5 cm long.
  15a. Corolas de 3–6 mm long. .... *J. comata*
  15b. Corolas de más de 6 mm long.
    16a. Cáliz 5-partido.
      17a. Inflorescencias generalmente terminales (a veces axilares también presentes).
        18a. Espigas capituliformes, condensadas en los extremos de las ramas. Brácteas y bractéolas largamente ciliadas. Semillas subesféricas .... *J. squarrosa*

18b. Espigas alargadas. Brácteas y bractéolas no largamente ciliadas. Semillas aplanadas .... *J. laevilinguis*

17b. Inflorescencias generalmente axilares.

19a. Hojas pecioladas, de 2.5–5(–7) cm lat.; plantas higrófilas.

20a. Inflorescencias pedunculadas más largas que las hojas.

21a. Corola de menos de 1.4 cm long. .... *J. glaziovii*

21b. Corola de más de 1.4 cm long.

22a. Flores blancas con mancha lila en la fauce .... *J. corumbensis*

22b. Flores lilacinas con mancha blanca en la fauce .... *J. kuntzei*

20b. Inflorescencias de igual longitud o más cortas que las hojas.

23a. Flores de ca. 1.5 cm long. con segmentos del cáliz de menos de 1 cm long. .... *J. jujuyensis*

23b. Flores de ca. 2 cm long. con segmentos del cáliz de más de 1 cm long. .... *J. phyllocalyx*

19b. Hojas de menos de 2.5 cm lat.; plantas xerófilas.

24a. Flores solitarias en las axilas de las hojas superiores.

25a. Cáliz acampanado con los segmentos soldados; hojas lanceoladas a lineares, de menos de 0.3 cm lat. .... *J. riojana*

25b. Cáliz con los segmentos libres; hojas lanceoladas a ovadas, de 0.5–1.5 (–2.5) cm lat. .... *J. tweediana*

24b. Flores reunidas en espigas con brácteas diferenciadas.

26a. Semillas tuberculadas.

27a. Hojas de 0.3–1.5 cm lat., cortamente pecioladas .... *J. hunzikeri*

27b. Hojas de 1.8–2.5 cm lat., largamente pecioladas .... *J. gilliesii*

26b. Semillas lisas .... *J. lilloana*

16b. Cáliz 4-partido.

28a. Flores solitarias en las axilas de las hojas superiores o de brácteas similares a las hojas .... *J. axillaris*

28b. Flores en inflorescencias multifloras con brácteas marcadamente diferenciadas, mucho menores.

29a. Inflorescencias generalmente de espigas simples.

30a. Hojas angostas, de menos de 1 cm lat. .... *J. polygaloides*

30b. Hojas de más de 1 cm lat.

31a. Hojas con lámina ovada a orbicular, de 2.5–5.5 cm long. .... *J. cuspidulata*

31b. Hojas con lámina angostamente ovada, ovado-lanceolada o lanceolada, de 4–7 cm long.

32a. Espigas de 4–6 cm long.; corolas de ca. 0.8 cm long. Hojas de 1–2 cm lat., generalmente pubescentes .... *J. pectoralis*

32b. Espigas de hasta 12 cm long.; corolas de 0.8–1.2 cm long. Hojas de 1.5–2.5 cm lat., generalmente glabras .... *J. yhuensis*

29b. Inflorescencias compuestas de espigas agrupadas en racimos (raramente espigas simples en las axilas de las hojas).

33a. Inflorescencias con los ejes y las brácteas glandulosos.

34a. Lámina ovada o elíptica de 7–15 cm long.; espigas densas; brácteas de 3–5 mm long. .... *J. glutinosa*

34b. Lámina ovada de 3–10 cm long.; espigas laxas; brácteas de 2–3 mm long. .... *J. saltensis*

33b. Inflorescencias no glandulosas.

35a. Cáliz de ca. 0.6 cm long.; anteras con la teca apical perfecta y la basal obsoleta, reducida a un leve engrosamiento sobre el filamento .... *J. lythroides*

35b. Cáliz de más de 0.6 cm long.; anteras con la teca apical perfecta y la basal reducida pero no obsoleta.

36a. Brácteas, bractéolas y segmentos del cáliz albo-marginados. Corola de ca. 2.5 cm long. .... *J. hassleri*

36b. Brácteas, bractéolas y segmentos del cáliz totalmente verdes. Corola de 1–2 cm long.

37a. Corola de 1.5–2 cm., con tubo largo de 1–1.5 cm long. .... *J. goudotii*

37b. Corola de ca. 1 cm, con tubo corto de 0.5–0.6 cm long. .... *J. oblonga*

1. Justicia aequilabris (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 350. 1895. *Orthotactus aequilabris* Nees, in Martius, Fl. Bras. 9: 134. 1847. *Amphiscopia aequilabris* (Nees) Nees, in DC., Prodr. 11: 358. 1847. *Jacobinia aequilabris* (Nees) Lindau, Bull. Herb. Boissier 3: 486. 1895. TIPO: Brasil, s. loc., *Sellow 174* (holotipo, B destr., fot. F 8902!).

Orthotactus strobilaceus Nees, in Martius, Fl. Bras. 9: 133. 1847. *Amphiscopia strobilacea* (Nees) Nees, in DC., Prodr. 11: 358. 1847. *Justicia strobilacea* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 350. 1895. TIPO: Brasil. Pernambuco: fl. San Francisco, in sylvis at S. Antonio et Alegre praedia, *Martius* (sintipo, M!); Bahia, *Blanchet 2575* (sintipo, W!; isosintipos, BM!, K!, NY!).

Orthotactus arnottianus Nees, in Martius, Fl. Bras. 9: 132. 1847. TIPO: Brasil. Bahia: *Blanchet 2575* ex herb. Delessert (isotipo, E!).

Orthotactus venosus Nees, in Martius, Fl. Bras. 9: 133. 1847. *Amphiscopia venosa* (Nees) Nees, in DC., Prodr. 11: 358. 1847. *Justicia venosa* (Nees) Graham, Kew Bull. 43 (4): 617. 1988. TIPO: Brasil. Río Maranhao: *Pohl 1849* (holotipo, W!, fot. US!).

Jacobinia velutina Lindau, Bull. Herb. Boiss. 3: 487. 1895. *Justicia velutina* (Lindau) Lindau ex Hassler, Add. Pl. Hassl.: 6. 1917. TIPO: Brasil. *Glaziou 13076* (isotipos, K!, R!).

Jacobinia glabribracteata Lindau, Bull. Herb. Boissier 3: 486. 1895. *Justicia glabribracteata* (Lindau) Graham, Kew Bull. 43 (4): 617. 1988. TIPO: Bolivia. Santa Cruz: 600–800 m, *Kuntze s.n.* (holotipo, B destr., fot. F 8906!; isotipo, NY!).

Sufrútice de 0.3–0.5 m alt., con tallos subcilíndricos, pubérulos. Hojas con pecíolo de 0.7–1.5 cm long., pubérulo, y lámina ovada a anchamente elíptica, de 4–9 cm long. por 2.5–5 cm lat., cuneada y decurrente en la base, aguda u obtusa en el ápice, levemente pubérula en el haz, velutino pubérula en el envés. Infloresencencias en espigas de 5–7 cm long., subsésiles y alternas en las axilas de las hojas superiores; brácteas imbricadas, ovadas, de 1.3–1.7 cm long. y 0.7–0.9 cm lat., con la venación marcada, muy levemente pubérulas, ciliadas; bractéolas lanceoladas de ca. 1 cm long. y 2 mm lat., glabras, ciliadas. Cáliz profundamente 5-partido, con los segmentos lanceolados, de ca. 5 mm long., generalmente glabros. Corola roja de 3–3.5 cm long., con tubo basal angostamente cilíndrico, de 2.5 cm long. y hasta 4 mm diám., el labio posterior bidenticulado, de 1 cm long. por 3.5 mm lat., el anterior trilobado, de ca. 1 cm long., con los lóbulos de 6–7 mm long. Estambres exertos con las anteras debajo del ápice del labio superior, las tecas a distinta altura, ambas de ca. 2 mm long., múticas. Cápsula claviforme de ca. 1 cm long., con semillas aplanadas y (según Nees, 1847a) tuberculado-verrugosas de ca. 2 mm long.

Ilustraciones. Nees, 1847a: tab. 21 (sub *Orthotactus venosus*).

Distribución, hábitat y fenología. Este de Bolivia, Brasil y noreste de Paraguay, en la región del Amambay. Habita en bordes de bosque y florece en primavera, de octubre a noviembre.

Justicia aequilabris se caracteriza por las espigas axilares con brácteas imbricadas, ovadas, anchas y papiráceas, y las flores de corola roja generalmente de más de 3 cm long. Es una especie variable y de distribución amplia (ver tipos citados en sinonimia), aunque aparece raramente y está relativamente poco coleccionada, como lo demuestra la falta de ejemplares de Bolivia y Brasil en los herbarios. Los nombres que se consideran sinónimos presentan ejemplares tipo cuyas pocas diferencias parecen formar parte de la variabilidad morfológica de esta especie.

Material seleccionado. PARAGUAY. **Amambay:** In dumetis Ponta Porá, Sierra de Amambay, *Rojas 10929* (G). **Concepción:** Zwischen Rio Apa und Rio Aquidaban, Centurion, *Fiebrig 4103* (BM, E, G, P).

2. Justicia axillaris (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 350. 1895. *Rhytiglossa axillaris* Nees, in Martius, Fl. Bras. 9: 122. 1847. TIPO: Brasil. Rio Grande do Sul: fl. Jacuy ad S. Barbara da Encruzilhada, *Sellow s.n.* (holotipo, B destr., fot. F 8811!).

Rhytiglossa campestris Nees, in Martius, Fl. Bras. 9: 118. 1847. *Justicia campestris* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4 (3b): 350. 1895, non *Justicia campestris* Griseb., Goett. Abh. 19: 225. 1874. TIPO: Brasil. Rio Grande do Sul: Porto Allegre et Catalao, *Sellow s.n.* (holotipo, B destr., fot. F 8813!; probables isotipos, E!, K!).

Hierba pequeña, rizomatosa, de hasta 15(–30) cm alt., con tallos erectos o algo decumbentes, subcilíndricos, delicados, con dos líneas longitudinales y opuestas de pubescencia fina y curva en cada entrenudo, surgiendo de las axilas de las hojas, y raíces engrosadas. Hojas subsésiles a cortamente pecioladas, las inferiores orbiculares a ovadas, de 1.5–2.5 cm long. y 1–1.5 cm lat., redondeadas, las superiores ovadas o angostamente ovadas a elípticas (raramente orbiculares), de 1–2 cm long. y 0.3–1 cm lat., agudas, todas glabras o hirsuto-pubérulas, cilioladas en el margen. Flores bibracteoladas sésiles en las axilas de las hojas superiores o de brácteas algo más angostas y pubescentes, poco diferenciadas, a veces formando espigas terminales; bractéolas lanceoladas, de 0.7 a 1.5 cm long. y ca. 1 mm lat., pubérulas, ciliadas. Cáliz profundamente 4-partido con los segmentos lineales, de 0.5–1 cm long., generalmente ciliados. Corola lila, pálido-lilacina a blanquecina de 1.4–1.7 cm long., pubérula. Labios de aproximadamente la misma longitud que el tubo basal, el posterior brevemente bidentado, el anterior profundamente trilobado, con los lóbulos de 5–6 mm long. y 3 mm lat., el lóbulo central más ancho y venoso-rugoso en la fauce. Estambres con las tecas divergentes, y estilo filiforme

con estigma bilobado. Cápsula claviforme, de 7 mm long. y 2 mm diám., glabra. Semillas algo aplanadas, de 1.5–2 mm diám., amarillentas, tuberculado-verrugosas; retináculos de 2 mm longitud.

Ilustraciones. Dawson, 1979: 573.

Distribución, hábitat y fenología. Sur de Brasil, Uruguay, este de Argentina y Paraguay oriental, en campos abiertos arenosos o pedregosos. Florece en primavera y verano, de octubre a marzo.

Justicia axillaris y *Justicia campestris* parecen corresponder a formas con distinta morfologia foliar y diferente cantidad de pubescencia de una misma especie polimórfica característica de campos abiertos, por lo que el último nombre se trata como sinónimo del primero. Por su cáliz 4-partido, brácteas angostas y semillas tuberculadas, se clasifica en *Justicia* sect. *Dianthera* subsect. *Saglorithys* (Tabla 1). *Justicia reitzii* Leonard (Tipo: Brasil. Santa Catarina: Abelardo Luz, 11 km ao Norte de Abelardo Luz, campo, 500–600 m, 25 Dic. 1956, *Smith y Reitz 9230,* holotipo, US!) es una especie rara del sur de Brasil muy afín a *J. axillaris,* que se diferencia por las flores siempre solitarias en las axilas de las hojas superiores y el tamaño generalmente menor y la textura más coriácea de sus láminas foliares. A pesar de que recientemente se citó como sinónimo de *J. axillaris* (Ezcurra, 1999), se considera que las relaciones entre ambas deberían establecerse sobre la base del estudio de más material del sur de Brasil.

Material seleccionado. ARGENTINA. **Corrientes:** Concepción, palmar, *Arbo 906* (CTES); Ituzaingó, Ea. El Plata, *Meyer 6414* (LIL); Santo Tomé, Gdor. Virasoro, Establ. Timbauva, a más o menos 9 km de R 14, monte próximo al casco, *Romanczuk 188* (SI); San Miguel, 21 km al S de Loreto, *Schinini 8327* (CTES); Ituzaingó, Playadito, 20 km W de Apóstoles, *Schinini 21794* (CTES); San Roque, M. P. Mansilla, *Ybarrola 2866* (LIL). **Entre Ríos:** Concordia, Ayuí, alrededores Hotel Salto Grande, flor lila, campos pedregosos, *Troncoso 1158* (SI); Federación, Salto Grande, laderas pedregosas, *Troncoso 27231* (SI); La Paz, La Paz a Feliciano, *Troncoso y Bacigalupo 3337* (SI). **Misiones:** Capital, Posadas, sabana, *Burkart 14171* (SI); Apóstoles, Apóstoles, campos, *Burkart 14280* (SI); Bonpland, campos, *Jörgensen 698* (LIL); Candelaria, *Ruiz Huidobro 4876* (LIL). PARAGUAY. **Alto Paraná:** Estancia Santa Elena, Pira Pyta, *Schinini y Caballero Marmori 27168* (CTES). **Caaguazú:** Pr. Caaguazú in campo sicco, *Hassler 9271* (G). **Canindeyú:** in regione Yerbalium de Maracayú, Paraguaria euro austral, *Hassler 5108* (BM, G). **Cordillera:** in fluminis Y-acá, in campo pr. Valenzuela, *Hassler 6813a* (G); in valle fluminis Y-acá, in campo pr. Valenzuela, *Hassler 7106* (G). **Paraguarí:** in valle fluminis Y-acá, in campo pr. Chololó, *Hassler 6813* (G). **S. dep.:** Paraguaria centralis, *Hassler 2962* (BM, G, NY); 'Plantae Paraguariensis', *Hassler 1907* (G).

3. Justicia baenitzii (H. Winkler) C. Ezcurra, Bol. Soc. Argent. Bot. 25(3–4): 348. 1988. *Beloperone baenitzii* H. Winkl., in Fedde Repert. Nov. Spec. 7: 113. 1909. TIPO: Bolivia. San Carlos bei Mapiri, in Walden, 750 m, Ago. 1907, *Buchtien 1409* (holotipo, B destr., fot. F 8922!; isotipo, US!).

Beloperone viridissima Rusby, Mem. New York Bot. Gard. 7: 367. 1927. TIPO: Bolivia. Huachi, 1800 ft., 13 Ago. 1921, *White 550* (holotipo, NY!; isotipo, US!).

Sufrútice perenne, a veces decumbente o apoyante, de cerca de 1 m alt., con ramas cilíndricas, levemente 4-sulcadas, geniculadas por encima de los nudos, glabras o pubérulas. Hojas con pecíolo de 1–3 cm long. y lámina ovada o anchamente elíptica de 8–20 cm long. por 3–7 cm lat., generalmente glabra, acuminada en el ápice, cuneada y algo decurrente en la base, lisa a ondulado-crenada en el margen, con las venas principales pubérulas y prominentes en el envés. Flores en espigas unilaterales laxas agrupadas en racimos axilares y terminales que superan ampliamente a las hojas en longitud. Raquis pubérulo; brácteas de las espigas lanceolado-lineales de 2–4 mm long., glanduloso-pubérulas; bractéolas en las bases de las flores lineales, de 2 mm long., pubérulas. Cáliz de 3–4 mm long. con los 5 segmentos triangulares, agudos, de 2.5–3 mm long., glanduloso-pubérulos. Corola roja de 2.5–2.9 cm long., con tubo de cerca de 1.5 cm long., angosto, la garganta de 4 mm diám., los labios de 1.5 cm long., el posterior levemente bidentado, el anterior trilobado y levemente reticulado-venoso en la fauce. Estambres con filamentos de 1 cm long. y anteras con tecas desiguales, una de 1.5 mm long., la otra de más de 2 mm long., la superior mútica, la inferior apendiculada en la base. Cápsula inmadura claviforme, de ca. 1 cm long. por 2 mm diám., pubérula, con la mitad inferior angosta y aplanada y la mitad superior inflada y apiculada. Semillas maduras desconocidas.

Ilustraciones. Ezcurra, 1993a: 342.

Distribución, hábitat y fenología. Perú (fide Brako & Zarucchi, 1993) y Bolivia hasta el Norte de la Argentina en selvas de la provincia fitogeográfica de las Yungas. En Argentina ha sido encontrada únicamente en el extremo NW de la provincia de Salta, y en el departamento de Ledesma, en la provincia de Jujuy. Es frecuente en el sotobosque de la selva entre los 600 y 1500 m s. mar, y florece en invierno y primavera, de julio a octubre.

Justicia baenitzii se asemeja al material tipo de *Jacobinia tenuistachys* Rusby (Tipo: Bolivia. Between Guanai and Tipuani, 1892, *Bang 1441,* ho-

lotipo, NY!; isotipo, E!) en la morfología de la inflorescencia y el tamaño de las hojas. Sin embargo el tipo de *J. tenusitachys* no presenta flores desarrolladas y además tiene hojas sésiles, por lo que no parece tratase de la misma especie.

Material seleccionado. ARGENTINA. **Jujuy:** San Martín, PN Calilegua, Río Las Piedras, *Iudica y Ramadori 354* (SI). **Salta:** Santa Victoria, PN Baritú, Nacientes del Santa Rosa, *Hilgert 759* (SI), *Hilgert 766* (SI); Santa Victoria, camino de Los Toldos a Lipeo, desvío hacia aguas termales, *Ahumada 8234* (SI); Orán, Río Pescado, a 9 Km de la finca de Yacúlica, *Vervoorst y Cuezzo 7725 C* (LIL); Orán, finca Candadito, 23 km from Aguas Blancas to Finca Yakulica, 450 m, *Wasshausen 1955* (K); Orán, Vado Hondo, *Willink 133* (LIL).

4. **Justicia brasiliana** Roth, Sp. Pl. Nov.: 17. 1821. *Beloperone brasiliana* (Roth) Bremek., Verh. Kon. Nederl. Akad. Wetensch. Amsterdam, Afd. Naturk. sect. 2, 45(2): 52. 1948. TIPO: Orig. de Brasil, cult. en Europa (no visto).

Justicia nodosa Hook., Bot. Mag. 56: tab. 2914. 1829. *Dianthera nodosa* (Hook.) Benth., in Bentham & Hooker, Gen. Pl. 2 (1): 1113. 1876. TIPO: Brasil. Cult. en Liverpool Bot. Gard. (holotipo, K!).

Beloperone amherstiae Nees, in Wallich, Pl. Asiat. Rar. 3: 102. 1832. TIPO: "Ex horto ill. Amherstiae specimina, a Bollokio in Indam orientalem translata," in herb. Wallich (fide Nees, 1847b) (no visto).

Beloperone amherstiae Nees var. *debilis* Nees, in Martius, Fl. Bras. 9: 139. 1847. TIPO: Brasil. "In sylvaticis edilis . . . pr. praedium Mineiros," *Martius s.n.* (sintipo, M!); Porto Allegre, *Sellow s.n.* (sintipo, B destr.; isosintipo, K!).

Beloperone amherstiae Nees var. *lanceolata* Nees, in Martius, Fl. Bras. 9: 139. 1847. TIPO: Brasil. Montis Butacaray, *Sellow 120* (holotipo, B destr.; isotipos, E!, K!).

Beloperone amherstiae Nees var. *ciliaris* Nees, in Martius, Fl. Bras. 9: 139. 1847. TIPO: Brasil. *Sellow 145* (holotipo, B destr.).

Beloperone amherstiae Nees var. *graciliflora* Nees, in Martius, Fl. Bras. 9: 139. 1847. TIPO: Brasil. In the woods of Rio Grande, *Tweedie 752* (holotipo, K!).

Sericographis squarrosa Nees, in DC., Prodr. 11: 364. 1847. TIPO: Brasil. Rio Grande do Sul: *Tweedie s.n.* (holotipo, K! fot. US!)

Jacobinia festiva Rizzini, Leandra 5(6): 36, fig. 5. 1975. TIPO: Brasil. Rio de Janeiro: Barra de Maricá, *Rizzini y Irene 21* (holotipo, RB!).

Arbusto o hierba sufruticosa robusta, de 1–2 m alt., con tallos erectos o apoyantes, cilíndricos, glabros. Hojas cortamente pecioladas, con láminas lanceoladas a angostamente ovadas, de (2.5–)4–10(–18) cm long. por (1–)2–3(–4) cm lat., las superiores menores, acuminadas en el ápice y obtusas a cuneadas en la base, coriáceas, discolores, enteras o algo crenadas, glabras a muy levemente pubérulas. Flores sésiles dispuestas en espigas densas simples o compuestas, de hasta 3–5 cm long., más cortas que las hojas, cortamente pedunculadas y opuestas en las axilas de las hojas superiores. Brácteas axilantes de las flores oblanceoladas a espatuladas o lineales, de 8–12 mm long. por 1–2(–3) mm lat., una fértil y la otra estéril en cada nudo, glabras a levemente pubescentes; bractéolas lineales a lanceoladas de ca. 5 mm long. por 0.5 mm lat., semejantes a las brácteas. Cáliz profundamente 5-partido, de 4–5 mm long., con los segmentos lanceolados, de 3–4 mm long., agudos. Corola roja de 3–4.5 cm long., con tubo de ca. 2.5 cm long., estrecho, de hasta 5 mm diám. en la fauce, y labios de 1–1.5 cm long., el posterior erecto, angostamente ovado, levemente bilobado, y el anterior patente, trilobado, con los lóbulos de 3–5 mm long. por 2–3 mm lat., redondeados. Estambres más cortos que el labio posterior, con las tecas a distinta altura, de ca. 2 mm long., la inferior sub-oblicua. Estilo filiforme con estigma bilobado, y ovario glabro. Cápsula claviforme castaño-brillante, de 1–1.3 mm long., con la mitad inferior sólida y lateralmente estrechada, y la superior subesférica, de 4 mm diám. Semillas aplanadas de contorno orbicular, de ca. 3 mm diám., lisas, pardo-claras, con un reborde en su cara interna; retináculos de ca. 2 mm long.

Ilustraciones. Wasshausen y Smith, 1969: 96 (fig. 14A).

Distribución, hábitat y fenología. Sur de Brasil, norte de Uruguay, noreste de Argentina y Paraguay oriental, desde el nivel del mar hasta los 600 m. Es una especie higrófila que habita en claros y bordes de bosques húmedos y en selvas, frecuentemente en lugares alterados como márgenes de ríos y bordes de picadas. Florece principalmente en verano y otoño, desde noviembre a mayo.

Justicia brasiliana se caracteriza por sus flores angostas de color carmín de hasta 4.5 cm long. dispuestas en inflorescencias axilares densas, con brácteas oblanceoladas a espatuladas o lineales. Es una de las Acantáceas más frecuente en bosques húmedos de Paraguay oriental y del sur de Brasil y este de Argentina, y por sus flores llamativas, más coleccionadas en la región. A pesar de haber sido introducida en cultivo en Europa tempranamente en el siglo XIX bajo los nombres de *Justicia brasiliana* y *Justicia nodosa*, actualmente no se registra como planta cultivada en Argentina (Parodi & Dimitri, 1980).

Material seleccionado. ARGENTINA. **Corrientes:** Berón de Astrada, Berón de Astrada, Itapé, *Ruiz Huidobro 2128* (SI); Santo Tomé, Cuay Grande, *Ruiz Huidobro 4249* (LIL); San Martín, desvío Km 395,8 FCNEA, *Ruiz Huidobro 4301* (LIL); Capital, Ruta 5, 19 km del Triángulo,

Schinini y Martínez Crovetto 12771 (SI); Mburucuyá, Ea. Santa Ana, *Schwarz 94* (LIL); Concepción, Río Santa Lucía, *Schwarz 9275* (LIL); CT, Dpto. Saladas, Ayo. Ambrosio, *Schwarz 9394* (LIL). **Chaco:** CH, Resistencia, Margarita Belén, *Aguilar 566* (LIL); Libertad, ruta 16, a orillas del Río Negro, *Legname 6052* (LIL); Libertad, Colonia Popular, *Schultz 16244* (SI). **Formosa:** Mojón de Fierro, *Krapovickas 1086* (SI); Formosa, Ruta 11 vieja, pasando Arroyo F. Cué hacia el N, *Guaglianone 726* (SI); Pilcomayo, Puerto Ramos, *Morel 7182* (LIL); Pilagá, Pilagá, *Pierotti 4204* (LIL); Pirané, Guayacán, *Reales 94* (LIL). **Misiones:** San Javier, costas Río Uruguay, *Bertoni 2513* (LIL); Guaraní, entre Gob. Morales y Fracrán, *Cabrera y Sáenz 29211* (SI); L. Alem, 7 Km E de L. Alem, lote 106, *Maruñak 678* (LIL); Oberá, Oberá, Villa Blanquita, *Mroginski 242* (LIL); San Martín, San Martín, *De Marco 10654 C* (LIL, M); San Ignacio, obraje EMA, *Schwarz 1639* (LIL); Iguazú, Ruta Nac. 101, 5 km del límite E del P. Nac., *Zuloaga 5270* (SI). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 6174* (BM, E, K, LIL, SI, US); Pr. Escuela Técnica Forestal, km 12 Puerto Stroessner, *Bernardi 18891* (BM, G, MO, NY). **Amambay:** Parque Nacional Cerro Corá, al lado del río Aquidabán cerca del fortín militar, *Brunner 1534* (G, MO, US); Pedro Juan Caballero, Tres Palos ad septentr., *Bernardi 19330* (G, MO, NY). **Caaguazú:** Arroyo Yakare'i, along N side from route 2, *Zardini y Aguayo 10730* (MO, US); Tebicuary Mí, in nemore collino Isla Alta, *Bernardi 18720* (G, MO, NY). **Caazapá:** Tavai, 500 m de Y-hovy, *Soria 3894* (CTES); R. Pirapó, N of José Fassardi, *West 8537* (SI). **Canindeyú:** 10 km al W de Cruce Guaraní, *Fernández Casas y Molero 5855* (MO, NY); in regione yerbalium de Maracayu, Paraguaria euro-austra, *Hassler 5207* (BM, G, K, P, W). **Central:** L'Assomption, dans les lieux ombragés, *Balansa 2459* (K, P); Paraguay Centralis, reg. lacus Ypacaray, *Hassler 11740* (BM, E, G, K, LIL, MO, US). **Concepción:** entre Paso Horqueta y Concepción, *Krapovickas et al. 14227* (MO, US); Zw. Rio Apa und Rio Aquidaban, Villa Sana, *Fiebrig 4662* (BM, E, K, M). **Cordillera**: in regione lacus Ypacaray, *Hassler 11105* (BM, K, MO, US); Montes, San Bernardino, *Hassler 1593* (G, P, SI); on silvis pr. Cordillera de Altos, *Hassler 1579* (G, K, P, US); Paraguaria centralis, in silva San Bernardino, *Hassler 3016* (BM, G, K, MO, P, W). **Guairá**: Cordillera Ybytyruzú, Villa San Pedro, *Basualdo 1876* (MO); Road Melgarejo–Antena, 8 km S of Melgarejo, *Zardini 11349* (MO, US); Tororo, camino a Cerro Polilla, *Degen 1032* (G); Tororo, Cerro Acatí, *Soria 2588, 2637* (G); Villa-Rica, dans les bois, *Balansa 2459a* (P). **Itapúa:** Encarnación, Mboycaé, *Bertoni 4024* (LIL). **Misiones:** San Ignacio, Estancia Brusquetti, *Mereles 1198* (G). **Ñeembucú:** Pilar, Curupayty, *Meyer 15950* (LIL); Villa Pilar, Escuela Agrícola, *Schulz 7876* (LIL). **Paraguarí:** Acahay Massif, on rocks on SE peak, *Zardini et al. 12782* (MO, US); Cerro Mbatoví, in forest, *Zardini y Soria 4442* (MO, US); Cerro Palacios, *Soria 2242* (G); Lago Ypoa, bosque que bordea el lago, *Soria 2720* (G); Parque Nacional Ybycu'i, forest on trail, *Zardini y Velásquez 12094* (MO); Yaguarón, Cerro Curupaytí, *Arenas 1189* (MO). **Presidente Hayes:** in regione cursus inferioribus fluminis Pilcomayo, *Rojas 664* (G); Ruta Trans Chaco, km 120, *Mereles 3904* (US). **San Pedro:** 10 km N de San Estanislao, *Krapovickas et al. 13889* (US); Loma Hoby, *Woolston 193* (SI), *Woolston 193C* (K). **S. dep.:** Central Paraguay, *Morong 200a* (BM, G, K, MO, US).

5. Justicia carnea Lindley, Bot. Reg. 17: t. 1397. 1831. *Ethesia carnea* (Lindl.) Raf., Fl. Tellur. 4: 63. 1838. *Jacobinia carnea* (Lindl.) Nicholson, Ill. Dict. Gard. 2: 206. 1885. TIPO: Brasil. Rio de Janeiro: enviado a Inglaterra e introducido en cultivo, ilustrado en Lindley (1831).

Cyrtanthera magnifica Nees, in Martius, Fl. Bras. 9: 100, t. 14. 1847. *Jacobinia magnifica* (Nees) Voss, Vilm. Blumengartn. (ed. 3) 1: 810. 1894. *Jacobinia magnifica* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 351. 1895. TIPO: Brasil. Rio de Janeiro: Tijuca, *Schott s.n.* (holotipo, W!).

Cyrtanthera magnifica Nees var. *minor* Nees, in Martius, Fl. Bras. 9: 100. 1847. TIPO: Brasil. Semidorio, *Riedel s.n.* (isosintipo, BR, fot. US!); Rio de Janeiro, Corcovado, *Luschnath s.n.* (sintipo, LE no visto).

Cyrtanthera pohliana Nees, in Martius, Fl. Bras. 9: 101. 1847. *Jacobinia pohliana* (Nees) Voss, Vilm. Blumengartn. (ed. 3) 1: 810. 1894. *Jacobinia pohliana* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 351. 1895. TIPO: Brasil. S. est.: pr. Mideiros et Entre dos Morros, *Pohl 196* (sintipo, W!); Minas Gerais: in silvis primaevis ad Cabo d'Agosto et Villa do Principe, *Martius s.n.* (sintipo, M!); Rio Grande: Porto Alegre, Serra de S. Antonio, *Sellow 97, 252* (sintipos, B destr.); Tres Irmâos, *Sellow 214* (sintipo, B destr.); Praesidio São João Baptista, *Sellow 254* (sintipo, B destr., fot. F 8915!, isosintipo, K!).

Cyrtanthera pohliana Nees var. *obtusior* Nees, in Martius, Fl. Bras. 9: 101. 1847. *Jacobinia obtusior* (Nees) L. H. Bailey, Gentes Herb. 1: 136. 1923. TIPO: Brasil. "Absque loco natalis. . .," *Raven* (sintipo, M!); Ins. Sta. Catarina, *Chamisso s.n.* (sintipo, LE no visto).

Cyrtanthera pohliana Nees var. *velutina* Nees, in Martius, Fl. Bras. 9: 101. 1847. *Jacobinia velutina* (Nees) Voss, Vilm. Blumengartn. (ed. 3) 1: 810. 1894. TIPO: Brasil. Rio de Janeiro: "flowers a fine rose colour," *Tweedie s.n.* (sintipo, K!); Argentina. Buenos Aires: "one of the . . . ornaments of the gardens of Bs Ays flowers all the year," *Tweedie s.n.* (sintipo, K!).

Orthotactus ciliatus Nees, in Martius, Fl. Bras. 9: 135. 1847. *Amphiscopia ciliata* (Nees) Nees, in DC., Prodr. 11: 359. 1847. TIPO: Brasil. Rio de Janeiro: Monte Corcovado, *Luschnatt s.n.* in herb. Martius (holotipo, M!).

Arbusto o hierba sufruticosa robusta de hasta 2 m alt., con ramas subtetrágonas, glabras o cortamente pubescentes. Hojas con pecíolo de 3–5 cm long. y lámina ovada o elíptica de 10–25 cm long. por 5–8 cm lat., obtusa y levemente acuminada en el ápice, cuneada en la base, parcialmente decurrente sobre el pecíolo, de textura herbácea, áspera, con el margen irregularmente crenado, con las venas principales marcadamente prominentes y notorias en el envés, las secundarias arqueadas y paralelas, la nervadura en general pubescente. Flores sésiles dispuestas en tirsos terminales densos y bracteados, ovoides, de 10–20 cm long. y 5–8 cm diám., floribundos. Brácteas foliáceas; bractéolas

lanceoladas, de aprox. 15 mm long. por 2 mm lat., obtusas, glabras y ciliadas. Cáliz profundamente 5-partido, con los segmentos lanceolados, de 10 mm long. por 2 mm lat., agudos. Corola rosada o roja, de cerca de 5–6 cm long., con tubo de ca. 3 cm long., ensanchado a 3–4 mm diám. en la garganta, y labios de ca. 2.5 cm long., el posterior curvo y bidentado, el anterior patente y trilobado, con los lóbulos de 3 mm long. Estambres inclusos debajo del labio posterior, con filamentos de ca. 4 cm long., y anteras con tecas a distinta altura: la superior separada por el conectivo y oblicua, de ca. 3 mm long. ambas. Fruto desconocido.

Ilustraciones. Nees, 1847a: tab. 14 (sub *Cyrtanthera magnifica*). Wasshausen y Smith, 1969: 90, fig. 13B (sub *Jacobinia carnea*).

Distribución, hábitat y fenología. Sur de Brasil, noreste de Argentina y Paraguay oriental. Habita en bosques húmedos, en claros y bordes de picadas, frecuentemente en terrenos bajos y cerca de cursos de agua. Florece principalmente de primavera a otoño, entre noviembre y mayo.

Nombre vulgar. "Vara de la justicia" en Argentina (Parodi & Dimitri, 1980), "Plume flower" en Nueva Zelandia (Webb, 1995), "Brazilian plume" en Estados Unidos (Daniel, 1995).

Justicia carnea es una especie del sur de Brasil y regiones limítrofes cultivada como ornamental en lugares de clima cálido de todo el mundo por sus grandes inflorescencias de flores rojas o rosadas, que aparecen durante todo el año, hasta en ambientes sombríos. Su cultivo puede haber extendido su distribución natural original, ya que se ha asilvestrado en regiones donde ha sido introducida. Por ejemplo ha sido citada para Ecuador y Colombia (Leonard, 1951–1958; Wasshausen & Smith, 1969), y como introducida y naturalizada en Nueva Zelandia (Webb, 1995: 154).

Material seleccionado. ARGENTINA. **Misiones:** Iguazú, Salto Iguazú, *Rodríguez 789* (K, SI); General Manuel Belgrano, reserva estricta de San Antonio, *Múlgura 1891* (SI); San Pedro, reserva Esmeralda, *Deginani 1320* (SI); General Manuel Belgrano, San Antonio, 8 km de San Antonio, *Deginani 2080* (SI); San Javier, Arroyo Patiño, *Schwarz 4176* (LIL). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 5730* (BM, G, LIL, SI), *Fiebrig 5826* (G, LIL, SI); procedente puerto Bertoni, Alto Paraná, culta Jardín Botánico, *Rojas 10688* (LIL).

6. Justicia chacoënsis Wasshausen & C. Ezcurra, Candollea 52: 178. 1997. *Beloperone riparia* S. Moore, Trans. Linn. Soc. London, Bot. 4: 432. 1895, non *Justicia riparia* Kameyama, Bol. Bot. Univ. São Paulo 14: 204. 1995. TIPO: Brasil. Near Corumbá, *Moore 1047* (holotipo, BM!; isotipo, B destr., fot. F 8944!).

Arbusto o sufrútice ramoso de 0.80–1.50 m alt., con tallos glabros, ramificados, de corteza pálida. Hojas con pecíolo de 0.5–1.5 cm long. y lámina ovada a anchamente elíptica, de 6–13 cm long. y 2.5–6 cm lat., acuminada en el ápice, cuneada y decurrente en la base, algo discolor, glabra en el haz, velutino-pubérula y glabrescente en el envés. Inflorescencias en espigas densas, de 3–8 cm long., en las axilas de las hojas superiores, éstas a veces reducidas y entonces las espigas reunidas en un racimo apical denso, el conjunto oscureciéndose al secarse; brácteas angostamente lanceoladas, de 1–1.3 cm long. por ca. 1 mm lat., largamente acuminadas, pubérulas, negras al secarse; bractéolas lineales, de 3–5 mm, más angostas, pubérulas. Cáliz profundamente 5-partido, con los segmentos lanceolados, de 4 mm long. por menos de 1 mm lat., agudos, pubérulos. Corola de ca. 4.5 cm long., roja, con tubo angostamente cilíndrico de 2–2.5 cm long. y labios de 1.5–2 cm long., el posterior angostamente oblongo, agudo, el anterior de 0.8 cm long., profundamente trilobado, con los lóbulos angostamente oblongos, de 0.7–1 cm long. y 3 mm lat., redondeados. Estambres exertos casi hasta el ápice del labio posterior, las anteras con las tecas marcadamente superpuestas, de ca. 2 mm long., las inferiores separadas de las superiores ca. 2 mm, algo menores y basalmente apiculadas. Cápsulas angostamente claviformes, de 1–1.3 cm long. por 2–3 mm lat., con la base sólida y lateralmente estrechada en el tercio inferior, muy levemente pubérulas. Semillas aplanadas, de 2 mm diám., verrucosas, oscuras; retináculos de ca. 1 mm long.

Ilustraciones. Figura 5.

Distribución, hábitat y fenología. Sudoeste de Brasil, norte de Paraguay y regiones limítrofes de Bolivia. Habita en bosques xerófilos abiertos, y florece en primavera y otoño, de septiembre a mayo.

Justicia chacoënsis se caracteriza por sus flores rojas grandes, de cerca de 5 cm long., en inflorescencias espiciformes con brácteas pequeñas y angostas que oscurecen al secarse. Por sus características morfológicas se ubicó en *Justicia* sect. *Orthotactus* (Wasshausen & Ezcurra, 1997).

Material seleccionado. PARAGUAY. **Chaco:** Agua Dulce, *Schinini y Bordas 18090* (G, MO); Capitán Pablo Lagerenza, Pique Histórico, ca. 10 km SE de P. Lagerenza, *Charpin y Ramella 21610* (G); Cerro León, *Schinini y Bordas 17794* (US); Cerro León, desde lomada al S (campamento) hasta meseta Central, *Charpin y Ramella 21742* (G); Fortín Gabino, Mendoza a Lagerenza, a 12 km. desvío a Parque Cué, *Degen 3280* (FCQ); Mayor Pedro Lagerenza, en bosque abierto de quebracho y samohú, *Schinini y Bordas 14999* (US); Palmar de las Islas a Ravelo, Cerro san Miguel, *Mereles y Ramella 2795* (FCQ, G).

Figura 5. *Justicia chacoënsis.* —A. Rama con flores. —B. Flor con bráctea, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. *Fortunato 3738* (G), *Billiet y Jadin 3263* (G).

7. **Justicia comata** (L.) Lamarck, Encycl. 1: 632. 1785. *Dianthera comata* L., Syst. Ed. 10: 850. 1759. *Leptostachya comata* (L.) Nees, in DC., Prodr. 11: 381. 1847. *Ecbolium comatum* (L.) Kuntze, Revis. Gen. Pl. 2: 487. 1891. *Stethoma comata* (L.) Britton, Bot. Porto Rico 6: 218. 1925. *Psacadocalymma comatum* (L.) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk, Tweede Sect. 45: 55. 1948. TIPO: Jamaica. *Browne s.n.* (lectotipo, designado por Graham (1988), LINN, microficha BM!).

Leptostachya martiana Nees, in Martius, Fl. Bras. 9: 152. 1847. TIPO: Brasil. Bahia: *Martius s.n.* (sintipo, M!), *Salzmann s.n.* (sintipo, B destr., fot. F 7835!; isosintipo, BM!); s. loc., *Sellow s.n.* (sintipo, B destr.; probable isosintipo, BM!); Pará, *Poeppig s.n.* (sintipo, B destr.). Cuba. S. loc.: *Poeppig s.n.* (sintipo, B destr.).

Leptostachya martiana Nees var. *hispida* Nees, in Martius, Fl. Bras. 9: 152. 1847. TIPO: Guyana Británica. *Schomburgk s.n.* (sintipo, K no visto).

Leptostachya martiana Nees var. *macrophylla* Nees, in Martius, Fl. Bras. 9: 152. 1847. TIPO: Guyana Británica. *Schomburgk s.n.* (holotipo, K!; isotipo, E!).

Leptostachya parviflora Nees, in Martius, Fl. Bras. 9: 151. 1847. TIPO: Brasil. Bahia: Ilheus, *Maximilianus Vied s.n.* (sintipo, BR no visto), *Sellow 125* (sintipo, B destr., probables isosintipos, K!, E!); Soteropolin, *Blanchet s.n.* (sintipo, G no visto; isosintipo, M!); Castelnovo, *Riedel s.n.* (sintipo, LE no visto).

Rhytiglossa acuminata Nees, in DC., Prodr. 11: 354. 1847. *Justicia acuminata* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3b): 351. 1895. TIPO: Mexico. Tabasco: marais de Teapa, *Linden 1633* (lectotipo, designado por Daniel (1995), K!).

Justicia humifusa Swartz, Prodr.: 14. 1788. TIPO: Jamaica. *Swartz s.n.* (holotipo, BM!, isotipo, M!).

Thalestris graminiformis Rizzini, Dusenia 3(2): 190. 1952. TIPO: Brasil. Paraná: Parque Nacional do Iguazú, *Duarte 1705* (holotipo, RB!; isotipo, NY!).

Hierba perenne, con largos rizomas horizontales provistos de raíces adventicias en los nudos, y tallos erectos de 30–80 cm alt., cilíndricos, frágiles, glabros o muy levemente pubérulos. Hojas opues-

tas, sésiles, subsésiles o cortamente pecioladas, angostamente ovadas, oblongas o lanceoladas, de 4–8(–15) cm long. por (0.8–)1–2 cm lat., redondeadas, cordadas o cuneadas en la base, frecuentemente decurrentes sobre el pecíolo, agudas, levemente discolores, glabras o pubérulas. Flores muy pequeñas dispuestas en espigas secundifloras laxas y delicadas que se agrupan formando seudoverticilos en inflorescencias paniculiformes laxas, terminales o axilares, con los ejes filiformes, glabros o levemente pubérulos, y con algunos pelos glandulares. Brácteas axilantes de las flores lanceoladas, de 0.8–1.2 mm long., generalmente glabras; bractéolas algo más pequeñas. Cáliz profundamente 5-partido, con los segmentos lanceolados, de 1–2.5 mm long. por menos de 0.5 mm lat., agudos, glabros o levemente glanduloso-pubérulos. Corola blanca, lilacina o violácea, de 3–6 mm long., glabrescente, con el tubo de 2 mm long., la garganta de 1 mm diám., los labios de cerca de 2.5 mm long., el posterior emarginado, el anterior trilobado, reticulado-rugoso en la fauce, con las marcas moradas, los lóbulos de aprox. 1 mm long. por 1 mm lat. Estambres con filamentos de ca. 2 mm long., y anteras con las tecas situadas a distinta altura, divergentes, de ca. 0.4 mm long., la inferior algo menor, separadas por el conectivo. Cápsula pubérula de 3–4(–7) mm long., con el tercio inferior sólido y lateralmente comprimido, la porción superior engrosada, de contorno oblongo. Semillas 4, aplanadas, orbiculares, de 1 mm diám., diminutamente verrugosas o pusticuladas, pardas; retináculos pequeños.

Ilustraciones. Ezcurra, 1993a: 352.

Distribución, hábitat y fenología. Ampliamente distribuida en América tropical desde el sur de México hasta Bolivia, Paraguay y norte de Argentina. En el sur de su distribución se encuentra entre el nivel del mar y los 600 m de altitud. Habita en suelos anegados de charcas, bañados, esteros y pantanos, o en lugares muy húmedos y soleados de bordes de bosques y selvas. También invade terrenos removidos húmedos y adopta características de maleza. Florece casi todo el año, principalmente en verano, de diciembre a febrero.

Justicia comata se caracteriza por las flores muy pequeñas dispuestas en inflorescencias paniculiformes tenues y laxas con ramificaciones verticiladas, de aspecto graminoide, y no tiene afinidades claras. Como varias otras especies higrófilas de ambientes anegados, es muy variable morfológicamente y tiene un área muy extendida, y eso ha dado lugar a la creación de numerosos nombres que resultan en su extensa sinonimia.

Material seleccionado. ARGENTINA. **Chaco:** Orillas del Río Guaycurú, *Meyer 2094* (LIL). **Corrientes:** General Paz, Lomas de Vallejos, *Krapovickas y Cristóbal 11812* (SI); Paso de los libres, Paso Troncón, *Ruiz Huidobro 3714* (LIL); Alvear, Ea. Santa Ana, costa Río Uruguay, *Schinini 16905* (LIL); San Martín, Yapeyú, costa Río Uruguay, *Ybarrola 1891* (LIL). **Formosa:** Guayculee, común en monte y esteros, *Jörgensen 2832* (SI); Guayculee, en chacras, *Jörgensen 3278* (SI); Pirané, al S del pueblo Pirané, *Morel 605* (LIL); Pilcomayo, Puerto Ramos, *Morel 7190* (LIL). **Jujuy:** Santa Bárbara, Ruta Prov. 1, Laguna San Miguel, *Kiesling 5618* (SI). **Misiones:** Iguazú, Cataratas del Iguazú, *Descole 3187* (LIL); San Ignacio, Jardín América, Saltos del Tabay, *Legname 5967* (LIL); Santa Ana, Santa Ana, bañados, *Rodriguez 755* (K, LIL); San Javier, Arroyo Itacaruaré, camino viejo, *Zuloaga 1944* (SI). **Salta:** Orán, Embarcación, km 1317, *Schreiter 11228* (LIL, SI); Orán, Campo Grande, 600 m, en un estero, *Venturi 5591* (K, SI). PARAGUAY. **Alto Paraguay:** Chaco, *Fiebrig 1423* (K, G, M). **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 6081* (G, K, LIL, SI, US); Río Monday, *Bertoni 1378* (LIL). **Amambay:** Bella Vista, Río Apa, *Schinini y Bordas 20628* (CTES). **Boquerón:** 20 km N de Coronel Oviedo, *Krapovickas 14312* (CTES, US); Tavaí, 3 km S del destacamento, Río Tebicuary, *Soria 3303* (CTES, MO). **Central:** Puerto Itá Enramada, arroyo cercano al Río Paraguay, *Schinini y Bordas 13314* (CTES, G, MO, US); San Lorenzo, Campus Universitario, *Mereles 1208* (CTES, G); Villa Rica dans les mares, *Balansa 2468* (G, K). **Concepción**: Zw. Rio Apa und Rio Aquidaban, Villa Sana, *Fiebrig 4688* (G, K). **Cordillera:** ad ripam lacus Ypacarai, *Hassler 3920* (BM, G, K, LIL, MO, NY, P); Cercanías de San Bernardino, *Mereles 3270* (G). **Guairá:** Colonia Independencia, *Schinini y Bordas 25242* (CTES, G); Común en el agua, Villa Rica, s.f., *Jörgensen 3796* (LIL, MO, NY, SI, US). **Itapúa:** Encarnación, Río Paraguay, Colonia Encarnación, *Montes 7157* (SI). **Misiones:** Santiago, Estancia La Soledad, Isla Carpincho, *Pedersen 5994* (K, MO, NY). **Presidente Hayes:** in regione cursus inferioris fluminis Pilcomayo, *Rojas 362* (BM, G, K); Ruta trans-Chaco, km 219, *Schinini y Palacios 25857* (CTES, G, K). **San Pedro:** Colonia Primavera, *Woolston 770* (K, LIL, NY, SI), *Woolston 1383* (K). **S. dep.:** Paraguaria Septentrionalis, *Fiebrig 4967* (G, K); s. loc., s.f., *Hassler 5985* (G, K, LIL, MO, NY, P).

8. Justicia corumbensis (Lindau) Wasshausen & C. Ezcurra, Candollea 52: 178. 1997. *Beloperone corumbensis* Lindau, Bull. Herb. Boissier ser. 2, 5: 373. 1905. TIPO: Brasil. Mato Grosso: pr. Corumbá, Abr. 1903, *Malme 3029* (holotipo, B destr., fot. F 8928!).

Hierba sufruticosa de 0.6–1 m alt., con tallos subcilíndricos, cuadrisulcados, pubérulos a glabros, a veces con dos líneas longitudinales pilosas en su juventud. Hojas con pecíolo de 0.5–1 cm long. y lámina ovada de 6–12(–18) cm long. por 2.5–5(–7) cm lat., aguda y acuminada en el ápice, obtusa a redondeada en la base, decurrente sobre el pecíolo, discolor, con cistolitos poco notorios en su superficie, subcoriácea, generalmente glabra. Flores sésiles dispuestas en espigas pedunculadas,

Figura 6. *Justicia corumbensis.* —A. Rama con flores. —B. Flor con bráctea, bractéolas, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. —D. Estilo y estigma. —E. Cápsula abierta. —F. Semilla. *Jörgensen 2337* (SI).

éstas solitarias o de a pares en las axilas de las hojas superiores. Espigas frecuentemente iguales o más largas que las hojas, densas, con pedúnculos de 2–4 cm long., y raquis a veces ramificado en la base; brácteas florales espatuladas a obovadas, de ca. 5 mm long. por 1.5–2.5 mm lat., acuminadas, foliáceas, generalmente glabras, desiguales en cada nudo, una fértil y la otra menor y estéril; bractéolas oblanceoladas, de menos de 5 mm long. Cáliz 5-partido, de 3–4 mm long., con los segmentos triangulares, de ca. 2 mm long., agudos, glabros, ciliolados en el margen. Corola blanca con marca lila en la fauce, de ca. 1.5 cm long., con tubo de 5–6 mm long. ensanchado en una garganta acampanada de 4 mm diám., y labios de 5–7 mm long., el posterior brevemente bidentado, erecto, cóncavo, de 4 mm lat., el anterior de 7 mm lat., ampliamente trilobado, patente, con los lóbulos de ca. 2.5 cm lat., redondeados. Estambres con filamentos de 4–6 mm long. y anteras con las tecas a distinta altura, la superior de 1.5 mm long., la inferior oblicua, algo mayor y con un apéndice glandular en la base. Estilo glabro; estigma redondeado y ovario glabro. Cápsula glabra o pubérula de ca. 1 cm long., con la mitad inferior sólida y lateralmente comprimida, y la superior subesférica y 4-seminada, de 3–4 mm diám. Semillas aplanadas, de contorno orbicular, de 2–3 mm diám., lisas, pardo-anaranjadas, con un reborde en su cara interna; retináculos de cerca de 2 mm longitud.

Ilustraciones. Figura 6.

Distribución, hábitat y fenología. Sudoeste de Brasil, sudeste de Bolivia, noreste de Argentina y oeste de Paraguay, principalmente en la región del Chaco. Habita a lo largo de los bosques ribereños de los ríos de la región chaqueña. Florece en verano, de enero a abril.

Justicia corumbensis pertenece a la sección *Plagiacanthus* y es una especie muy afín a *J. jujuyensis* C. Ezcurra (Wasshausen & Ezcurra, 1997) con la que suele confundirse en herbario. Ambas se asemejan en el tamaño, color y forma de las brácteas y flores, y en las características de los frutos. *Justicia corumbensis* se diferencia de *J. jujuyensis* por las flores en espigas pedunculadas frecuentemente más largas que las hojas axilantes, mientras que *J. jujuyensis* posee inflorescencias axilares más cortas. *Justicia jujuyensis* es característica de los bosques pedemontanos de transición entre las provincias fitogeográficas Chaqueña y de las Yungas, mientras que *J. corumbensis* generalmente habita en los bosques en galería de la región del Chaco septentrional.

Material seleccionado. ARGENTINA. **Chaco:** Maipú, ruinas km 75, ruta 95, *Schulz 15846* (CTES); Quitilipi, *Schulz 3235* (CORD, CTES). **Formosa:** Pirané: R. 90, 15 km al S de Pirané, *Guaglianone 680* (SI); Común en el monte, km 139 del F.C., *Jörgensen 2336* (LIL, SI), *2337* (SI); Patiño, Bartolomé de las Casas, *Schulz 16516* (CTES); Matacos, Ing. Juárez, Morello s.n. herb., *Schulz 18213* (CTES). PARAGUAY. **Alto Paraguay:** Colina Yaté, ca. 80 km ad meridiem Fuerte Olimpo, Alto Paraguay, *Bernardi 20457* (MO). **Presidente Hayes:** Estancia Maroma, a orillas del río Siete Puntas, *Degen y Mereles 3250* (FCQ); Km 326 de Asunción, haud procul ab Pozo Colorado, *Bernardi 20142* (G, MO, NY, US); Santa Elisa, *Hassler 2754* (BM, G, K, NY).

9. Justicia cuspidulata (Nees) Wasshausen, Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1253. 1993. *Rhytiglossa cuspidulata* Nees, in DC., Prodr. 11: 348. 1847. TIPO: Perú. *Mathews 3152bis* (holotipo, K!; isotipos, sub *Mathews 3152* BM!, B destr., fot. F 18412!).

Hierba sufruticosa en la base, rizomatosa, erecta, de hasta 50 cm alt., con tallos angostos, subcilíndricos, poco ramificadas, hirsuto-pubérulos. Hojas subsésiles con lámina ovada a orbicular, de 2.5–5.5 cm long. y 1.8–3 cm lat., obtusa o aguda en el ápice, truncada a levemente cordada en la base, glabra en el haz, y pubescente a pubérula en el envés. Inflorescencias en espigas terminales laxas de 7–17 cm long., con el raquis glanduloso-pubescente; brácteas triangulares de 3–4 mm long. por 1.5 mm lat., pilosas; bractéolas de la misma longitud, algo más angostas. Cáliz profundamente 4-partido, con los segmentos lineal-lanceolados, de 6–8 mm long., acuminados, pilosos. Corola lilacina de ca. 8 mm long., con tubo de 4 mm long. y 2 mm diám. en la fauce, y labios de 5 mm long., el posterior oblongo, de 2 mm lat., bidentado, y el anterior trilobado, con los lóbulos de 3 mm long. por 1.5 mm lat., redondeados. Estambres exertos hasta la mitad del labio superior, con las tecas superpuestas, oblicuas, marcadamente separadas por el conectivo. Cápsula de 8 mm long. por 2 mm de grosor, glabra. Semillas aplanadas, de 1 mm diám., diminutamente verrugoso-tuberculadas o pusticuladas, pardo-oscuras; retináculos de menos de 1 mm long.

Ilustraciones. Figura 7.

Distribución, hábitat y fenología. Originalmente descripta para Perú, se la ha encontrado en el este de Bolivia y en el noreste de Paraguay, en la región del Amambay. Probable en Brasil. Habita en bordes de bosque. Florece en primavera y verano, de agosto a marzo.

El material de Paraguay que aquí se determina con el nombre de *Justicia cuspidulata* pertenece a *Justicia* sect. *Dianthera* subsect. *Saglorithys*, un grupo de especies afines muy diversificado en América del Sur que se caracterizan por las inflorescencias en espigas simples y las flores medianas, con cáliz 4-partido y semillas tuberculadas (Tabla 1). A este grupo también pertenecen por ejemplo *Justicia rusbyana* Lindau (Bolivia. Yungas, *Bang 379*, isotipo, M!), *Justicia boliviana* Rusby (Bolivia. Vic. Cochabamba, *Bang 1225*, holotipo, NY!; isotipos, K!, US!), y la especie descripta como *Rhytiglossa piahuiensis* Nees (Brasil. Piahui, *Gardner 2290*, holotipo, K!; isotipo, BM!), especies muy afines a *Justicia cuspidulata*. La delimitación entre las especies de este grupo no es clara, y eso hace especialmente difícil asignarle un nombre al material de Paraguay. Por otro lado el tipo de *Justicia cuspidulata*, aunque morfológicamente muy similar al material de Paraguay, es de Perú, y existen pocos ejemplares que claramente parezcan pertenecer a esta especie en el área intermedia entre este país y Paraguay. Sin embargo, la flora del bosque tropical estacionalmente seco presenta distribución discontinua en Sudamérica, y existen varios otros ejemplos de especies de esta flora que presentan este tipo de distribución disyunta (Pennington et al., 2000). Por estas razones, antes de publicar un nombre nuevo para el material de Paraguay, prefiero identificarlo con el de *Justicia cuspidulata*, con el que está indudablemente relacionado. El nombre *Justicia amambayensis* C. Ezcurra que utilicé para esta especie en determinaciones en etiquetas de herbario hace unos años nunca fue publicado.

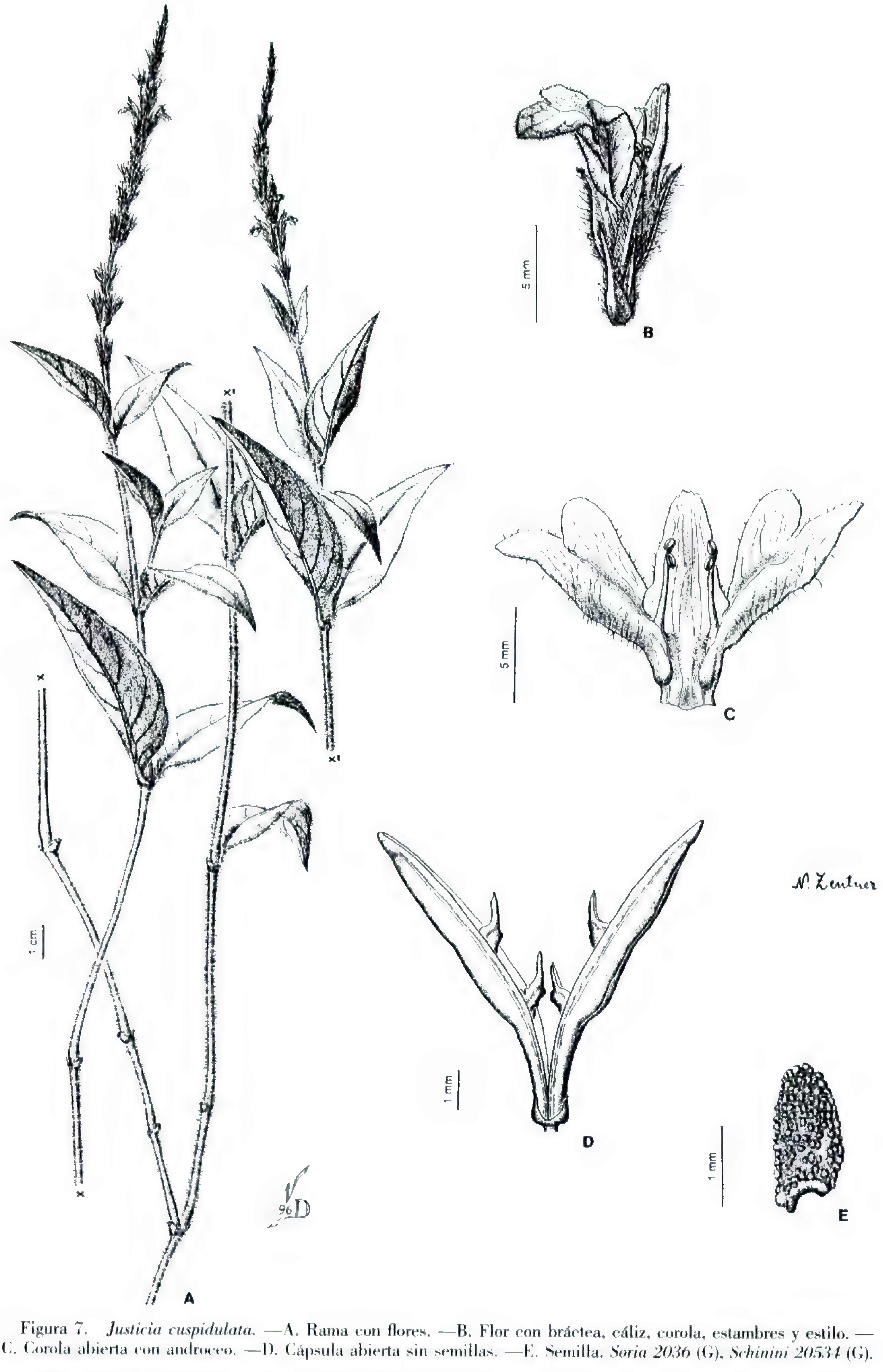

Figura 7. *Justicia cuspidulata.* —A. Rama con flores. —B. Flor con bráctea, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. —D. Cápsula abierta sin semillas. —E. Semilla. *Soria 2036* (G), *Schinini 20534* (G).

El tipo de *Rhytiglossa cuspidulata* (*Mathews 3152bis*) está mezclado con el de *Rhytiglossa hookeriana* (Perú. Chachapoyas, *Mathews 3152*), una especie con hojas más pequeñas y flores más angostas, como queda claramente explicitado en su descripción original, y los isotipos que se encuentran en BM tienen la identificación invertida.

Material seleccionado. BOLIVIA. **Santa Cruz:** Buenavista, desmontes chacras, *Steinbach 6973* (BM). **Beni:** Ballivián, Estación Biológica Beni, ca. 1/2 hour by trail N to R. Curiraba, *Solomon 14633* (M). PARAGUAY. **Amambay:** Amambay, Ruta 3 y Río Aquidabán, *Schinini y Bordas 20534* (CTES, US); in regione cursus superioris fluminis Apa, *Hassler 8003* (BM, G, NY), *7834* (BM, G, K, MO, NY, P); orillas del Río Aquidabán, ruta 3, *Krapovickas 45995* (CTES); Parque Nacional Cerro Corá, orillas de bosque, *Soria, Zardini y Ortiz 2036* (G, FCQ, MO); Zw. Río Apa und Río Aquidabán, *Fiebrig 4406* (BM, E, G, K, P); Caballero Cué, *Fiebrig 4473* (BM, E, G, K, P). **Cordillera:** Tobatí, Cerro Tobatí, *Arenas 287* (CTES); Tobatí, *Sparre y Vervoorst 1412* (LIL).

10. Justicia dumetorum Morong, Ann. New York Acad. Sci. 7: 193. 1893. TIPO: Paraguay. Río Pilcomayo, 1888–1890, *Morong 1538* (holotipo, NY!).

Beloperone kerrii N. E. Brown, Trans. Bot. Soc. Edinburgh 20: 67. 1896. TIPO: Argentina. Río Pilcomayo Expedition, 1890–1891, *Kerr 108* (holotipo, K!).
Beloperone albomarginata Lindau, Bull. Herb. Boiss., ser. 2, 5: 373. 1905. TIPO: Paraguay. Gran Chaco pr. Santa Elisa, Feb. 1903, leg. Rojas, *Hassler 2755* (holotipo, B destr., fot. F 8920!; isotipos, BM!, G!, K!, LIL!, MO!, NY!, P!, W!).

Hierba sufruticosa de 0.8–1.5 m alt., con ramas erectas, cilíndricas, longitudinalmente estriadas, engrosadas por encima de los nudos. Hojas con pecíolo de 0.5–2 cm long. y lámina ovada a lanceolada de 4–12 cm long. por 1–3 cm lat., aguda y acuminada en el ápice, cuneada o redondeada en la base, generalmente glabra, con cistolitos pequeños densamente esparcidos en su superficie. Espigas simples, densas, apicales y en las axilas de las hojas superiores, de 3–10 cm long., a veces agrupadas en racimos foliosos en el extremo de las ramas. Brácteas lanceoladas, opuestas, de 1–1.5 cm long. por 1.5–2 mm lat., glanduloso-pubérulas, con el margen blanquecino y hialino, cada una con una flor sésil en su axila y dos bractéolas de 7–9 mm long. en la base. Flores con el cáliz de la misma longitud que las bractéolas, profundamente 5-partido, los segmentos de 6–10 mm long. por 1.5 mm lat., glabros y albomarginados. Corola de color morado de 3–4 cm long. con tubo de 2–2.5 cm long., poco ensanchado en la fauce, y labios de 1.3–2 cm long., el posterior apenas emarginado, el anterior profundamente trilobado, con los lóbulos de 11 mm long. por 4–5 mm lat. Estambres con filamentos de 8 mm long. insertos en el ápice del tubo, y anteras con las tecas a distinta altura: la superior de 2 mm long., la inferior apenas más larga, y apendiculada en la base. Cápsula obovoide, de 1.5 cm long. por 0.6 cm diám., sólida y lateralmente estrechada en la mitad inferior, inflada y 4-seminada en el ápice. Semillas subesféricas, de 2–3 mm diám., castañas, lisas y lustrosas; jaculatores de 2.5 mm long., obtusos.

Ilustraciones. Figura 8.

Distribución, hábitat y fenología. Sudeste de Bolivia, Paraguay y norte de la Argentina, en la región del Chaco oriental. Habita en bordes y abras de bosque chaqueño, en lugares soleados con inundación periódica, y florece en primavera, verano y otoño, de octubre a mayo.

Justicia dumetorum se caracteriza por las flores rojas o moradas, de corola larga (3–4 cm), aparentemente polinizadas por picaflores. Existen algunos ejemplares de Paraguay y Bolivia que se citan con asterisco (*) en la lista de material (*Fiebrig 5074, Fiebrig s.138, Beck 5373* y *Troll 1688*) que se diferencian solamente por las corolas menores (de ca. 2 cm long.), lilacinas y de tubo basal más corto, con aspecto de ser polinizadas por abejas o abejorros (melitófilas). Estos ejemplares se asemejan bastante a *Justicia furcata* Jacq., especie descripta para México, y en algunos casos fueron determinados con ese nombre por Lindau en ejemplares de herbario (leg. *Fiebrig 5074* y *s.138*). *Justicia furcata* no habita en América del Sur (Wasshausen, com. pers.), y además estos ejemplares se diferencian de *Justicia furcata* del sur de Nortemérica y de América Central por las brácteas generalmente más anchas y las inflorescencias con menos flores. Sin embargo estos ejemplares coinciden mucho con especies afines descriptas para América del Sur como *Justicia peruviana* Lam. (ilustrada en Cavanilles, Icon. 1: 17, tab. 28. 1791, y Curtis Botanical Magazine 11–12: 430. 1797), *Justicia carthaginenesis* Jacq., y *Justicia lithospermifolia* Jacq.

Todas estas especies afines son muy variables, y en ellas se han encontrado formas con flores de distinto tamaño y diferente colorido (Leonard, 1951–1958; Daniel, 1995). Debido a ello coincido con Daniel (1995) en que el conjunto de estas especies de *Justicia* sect. *Simonisia* indudablemente aliadas a *Justica carthaginensis* Jacq. y a *Justicia furcata* Jacq. deberían ser objeto de un estudio de material abundante de toda su área de distribución, que incluya un análisis detallado de la forma y el color de la corola además de la distribución y el ambiente que habitan, requisitos indispensable para intentar diferenciarlas. Hasta tanto se realice

Figura 8. *Justicia dumetorum*. —A. Rama con flores. —B. Flor con bráctea, bractéolas, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. —D. Estilo y estigma. —E. Cápsula abierta. —F. Semilla. *Schulz 8673* (SI), *Saravia Toledo 10779* (SI).

ese estudio, trato al material de flores cortas y lilacinas que aparece en Bolivia y Paraguay como parte de la variabilidad intraespecífica de *Justicia dumetorum*.

Se aclara que el supuesto isotipo del nombre *Justicia kerri*, *Kerr 108*, que se encuentra en el herbario de Edimburgo (E), pertenece a *Justicia brasiliana* Roth y no concuerda con la descripcion original de *Justicia kerri*. Probablemente esté erróneamente etiquetado.

Material seleccionado. ARGENTINA. **Corrientes:** Itatí, Casa Cué, *Bernardello y Galetto 800* (SI); Dpto. San Cosme, 5 km E de Paso de la Patria, *Krapovickas y Cristóbal 11889* (SI). **Chaco:** Dpto. Resistencia, Barranqueras, *Meyer 16235* (LIL); Dpto. 1° de mayo, Colonia Benítez, *Schultz 8673* (SI). **Formosa:** abundante en el monte, *Jörgensen 2332bis* (SI); Dpto. Pilcomayo, Ruta 11, Clorinda a Formosa, Km 3, *Morel 1719* (LIL); Pozo del Tigre, *Parodi 8511* (LIL). **Salta:** Rivadavia, 18 km al E de Dragones, *Saravia Toledo 10779* (SI); Dpto. Orán, Embarcación, km 1317, *Schreiter 10866* (SI). BOLIVIA. **Beni:** Ballivián, Espíritu, en la zona de influencia del Rio Yacuma, sabana húmeda, *Beck 5373** (flor corta, lilacina) (US). **S. dep.:** Cañamina, Río La Paz, *Troll 1688** (M). PARAGUAY. **Boquerón:** Colonia Menno, Paratodo, *Arenas 1097* (LIL), *Arenas 1457* (US); Dr. Pedro P. Peña, 10 km al W del pueblo, *Spichiger et al. 2217* (G, US); Filadelfia, *Hahn 787* (US). **Chaco:** Mayor Pedro Lagerenza, *Schinini y Bordas 14973* (G, US). **Cordillera:** 2 km NE del Río Salado, de Limpio a Emboscada, *Arbo 1652* (CTES); Paso Correo, montes húmedos, orilla Río Salado, *Hassler 1650* (SI). **Concepción:** Zw. Rio Apa und Rio Aquidaban, Villa Sana, *Fiebrig 5074** (G, K). **S. dep.:** s. loc., *Fiebrig s.138** (G). **Presidente Hayes:** *Carter s.n.* (BM); Colonia Menno, Laguna Yaraguí, 7 km de Lolita, *Arenas 143* (US); in regione cursus inferioris fluminis Pilcomayo, *Rojas 81* (G, MO); pozo Colorado, *Mereles y Degen* 5563 (FCQ); Villa Hayes, *Zardini et al. 2592* (MO), *Zardini et al. 2593* (FCQ, MO, US).

11. Justicia floribunda (C. Koch) Wasshausen, Darwiniana 35: 151. 1998. *Libonia floribunda* C. Koch, Wochenschr. Ver. Bef. Gartenb. Kon. Preuss. Staat. 6: 266. 1836. TIPO: ilustración del ejemplar cultivado en el Jardín Botánico de Bruselas sobre el que se basó la descripción original en Morren, Belg. Hort. 14: 12. 1864 (lectotipo, designado por Wasshausen en Peixoto et al., 1998).

Sericographis pauciflora Nees, in Martius, Fl. Bras. 9: 109. 1847. *Justicia pauciflora* (Nees) Griseb., Abh. Konigl. Wiss. Gottingen 24: 262. 1879, non *Justicia pauciflora* Vahl, Eclog. Am. 1: 2. 1796. *Jacobinia pauciflora* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4 (3b): 351. 1895. *Justicia rizzinii* Wasshausen, Baileya 19: 3. 1973. TIPO: Brasil. S. loc., *Sellow s.n.* (sintipo, B destr., fot. F 8914!; probables isosintipos, E!, K!).

Sericographis pauciflora Nees var. *speciosor* Nees, in Martius, Fl. Bras. 9: 109. 1847. TIPO: Brasil. S. loc., *Tweedie s.n.* (sintipo, K!).

Arbusto ramoso de 0.50–1(–2) m alt., con ramas cilíndricas, pubérulas. Hojas con pecíolos de 0.4–1 cm long. y lámina ovada, elíptica a obovada, muy variable en tamaño, de 1.5–7 cm long. por 0.8–2.5 mm lat., las de cada par desiguales, las superiores mayores, obtusas y cuneadas, enteras a levemente aserradas, discolores, glabras o leve y cortamente pubescentes. Espigas paucifloras frecuentemente reducidas a flores solitarias sobre pedúnculos débiles hasta de 3 cm long. en las axilas de las hojas superiores, con brácteas y bractéolas triangular-lanceoladas, ca. de 1 mm long. por 0.5 mm lat., glabras a cortamente ciliadas. Cáliz 5-partido de 5 mm long., segmentos lanceolados, de 3.5 mm long., acuminados, pubérulos. Corola de 2–3 cm long., roja y con la mitad al tercio superior amarillo, tubo ca. de 20 mm long. por 5 mm diám. en la fauce, por fuera pubérulo, con algunos pelos glandulares, interiormente glabro; los labios oblongos, ca. de 5 mm long., el posterior erecto y obtuso o emarginado, el anterior erecto o algo patente y trilobado, con los lóbulos de ca. 2 mm long., triangulares. Estambres inclusos debajo del labio superior, filamentos pilosos en la parte media, anteras ca. de 2 mm long., algo superpuestas, oblicuas, caudadas. Ovario glabro o glanduloso-pubérulo en la porción apical, estilo glabro. Cápsula claviforme de 12–17 mm long. por 4 mm lat. y 2 mm de espesor, glabra o glanduloso-pubérula; semillas aplanadas, suborbiculares, ca. de 2 mm diám., castañas, levemente rugosas; retináculos, ca. de 2 mm long., obtusos.

Ilustraciones. Peixoto et al., 1998: 153.

Distribución, hábitat y fenología. Sur de Brasil y noreste de Argentina (este de Misiones). Tal vez también se encuentre en Paraguay oriental. Habita en selvas y bosques húmedos, especialmente sobre suelos periódicamente inundados, entre el nivel del mar y 1400 m de altitud. Florece en invierno, de mayo a agosto, y sus flores rojas de ápice amarillo probablemente sean polinizadas por picaflores.

Usos. Esta especie se cultiva como ornamental en regiones cálidas del mundo por sus llamativas flores rojas (Hay & Beckett, 1975, sub *Jacobinia pauciflora*). Las flores de esta especie se producen principalmente en invierno, y las plantas se reproducen fácilmente por gajos no floríferos y semillas (Parodi & Dimitri, 1980, sub *Jacobinia pauciflora*).

Nombre vulgar. “Bandera española” en Argentina (Parodi & Dimitri, 1980, sub *Jacobinia pauciflora*).

Justicia pauciflora se caracteriza por las flores ornitófilas con la corola roja de ápice amarillo. Parodi y Dimitri (1980, sub *Jacobinia pauciflora*) citaron a esta especie frecuentemente cultivada en Argentina como originaria de Brasil, por lo que cabe la posibilidad de que las poblaciones silvestres de Misiones hayan resultado de escapes de cultivo. Esto ha sucedido con otras especies de Acantáceas neotropicales cultivadas, que se han asilvestrado en regiones alejadas de su área de distribución original, como por ej. *Justicia carnea* Lindl. (en Nueva Zelandia, Webb, 1995) y *Ruellia breviflora* (Pohl) Ezcurra (en Asia y Australia, Ez-

curra, 1989). Sin embargo, es probable que las poblaciones silvestres de *Justicia floribunda* del este de Misiones se encuentren dentro del área de distribución natural de la especie, ya que ésta fue descripta originalmente para regiones contiguas del sur de Brasil (Nees, 1847a, 1847b; Wasshausen & Smith, 1969) y además ya existía en Misiones en el siglo XIX, como lo demuestra el ejemplar coleccionado por Niederlein en 1887.

Material seleccionado. ARGENTINA. **Misiones:** Bernardo de Irigoyen, *Hunziker, J. 950, 959* (LIL); Varana, territorio de Misiones, *Niederlein 1776* (LIL); Guaraní, Predio Guaraní, Arroyo Soberbio, borde del arroyo en barranca inundable, *Tressens et al. 5647* (SI); Gral. Manuel Belgrano, de Bernardo de Irigoyen a San Antonio pasando Salto Andresito, *Zuloaga 2111* (SI).

12. Justicia gilliesii (Nees) Bentham, in Bentham & Hooker, Gen. Pl. 2(2): 1109. 1876. *Adhatoda gilliesii* Nees, in DC., Prodr. 11: 395. 1847. TIPO: Argentina. San Luis: *Gillies s.n.* (sintipo, K!; isosintipo, E!); Santiago del Estero: "St. Iago de Cordova," *Tweedie 1260 p.p.*, mezcla con *Justicia tweediana* (sintipo, K!).

Justicia echegarayi Hieron., Bol. Acad. Nac. Ci., Córdoba 4(1): 61. 1881. TIPO: Argentina. San Juan: Dep. Zonda, Estancia Maradona, Ene. 1876, *Echegaray s.n.* (holotipo, CORD!).

Sufrútice ramoso de hasta 0.60 m alt., con ramas ascendentes o rastreras, cilíndricas, estriadas, pubescentes. Hojas pecioladas con pecíolos de 0.5–2 cm long., ovadas a elípticas, de 2.5–3 cm long. por 1.8–2.5 cm lat., agudas u obtusas y apiculadas, cuneadas en la base, membranáceas, generalmente pubescentes. Flores sésiles o cortamente pediceladas, con dos bractéolas en la base, solitarias en las axilas de brácteas, formando espigas de 4–12 cm long.; bractéolas elípticas de cerca de 1 cm long. por 2 mm lat.; brácteas de 9–12 mm long. por 4–5 mm lat., ambas glanduloso-pubescentes, ciliadas en el margen. Cáliz profundamente 5-partido, con los lóbulos angostamente ovados a lanceolados, subiguales, de 4 mm long., foliáceos, generalmente glabros. Corola celeste-lilacina a blanca de 2 cm long., pubérula, con tubo corto de cerca de 1 cm long., ensanchado en una garganta de aproximadamente 0.8 cm diám., los labios de 1–1.3 cm long., el anterior trilobado hasta la mitad, con la fauce blanca, convexa y transversalmente rugoso-venosa, con puntos morados. Estambres insertos en la base de la garganta, las anteras con las tecas subparalelas, una por encima de la otra, la inferior generalmente apendiculada en la base. Cápsulas obovoides, pubescentes, de 1.2–1.5 cm long. por 5–7 mm ancho, con la mitad inferior sólida y lateralmente comprimida. Semillas generalmente 4, suborbiculares, aplanadas, de 3–4 mm diám., pardas, diminutamente rugoso-tuberculadas; retináculos obtusos.

Ilustraciones. Figura 9.

Distribución, hábitat y fenología. Noroeste y centro de la Argentina, desde Catamarca, Tucumán, La Rioja, San Juan y Mendoza hasta Córdoba, San Luis y Santiago del Estero. Se la encuentra en montes áridos entre 300 y 1000 m s.m. Florece en verano y otoño, de diciembre a abril.

Nombre vulgar. "Albahaca de vaca" (Burkart, 1943, sub *Justicia echegarayi*).

Justicia gilliesii ha sido citada como de importancia como planta forrajera (Ariza-Espinar, 1971), al igual que varias otras Acantáceas del sur de Sudamérica (Burkart, 1943).

Material seleccionado. ARGENTINA. **Catamarca:** La Paz, el Divisadero, 13 Abr. 1947, *Brizuela 1132* (LIL); Ancasti, El Cajón, *Brizuela 1266* (LIL); Ambato, entre La Puerta y Huaicama, *Cristóbal 442* (LIL); Capital, Catamarca, *Nicora s.n.* (SI 18656); Camino a El Juncal, *Soriano 828* (SI); Paclín, entre Catamarca y Cuesta del Totoral, *Villa Carenzo 1119* (LIL). **Córdoba:** Tulumba, Salinas Grandes, ca. L. V. Mansilla, *Hunziker, A. 10985* (CORD); Cruz del Eje, entre Cruz del Eje y Villa Soto, *Hunziker, A. 12322* (CORD); Punilla, La Cumbre, *Nicora 1793* (SI). **La Rioja:** San Martín, Bajo Hondo, Campo Balde El Tala, Potrero 17, *Anderson 4044* (CORD); Chamical, Sierra de los Llanos, falda E, entre Chamical y la Aguadita, *Biurrun 1372* (CORD); Capital, La Rioja, *Burkart 12531* (SI); en las cercanías de San Carlos, camino a Córdoba, *Hieronymus y Niederlein 140* (CORD); Sierra de Velasco, camino al Dique Los Sauces, *Hunziker, A. 4721* (LIL); A. V. Peñaloza, Ruta 29, al S de Punta de los Llanos, entre el desvío a Tama y Carrizal, *Hunziker, A. 15096* (CORD); Famatina, Guanchín, *Venturi 7826* (SI). **Mendoza:** La Paz, Desaguadero, *Ruiz Leal 11819* (LIL). **San Juan:** Valle Fértil, N de Usno, *Kiesling 8961* (SI); Valle Fértil, camino a La Majadita, *Kiesling 5012* (SI). **San Luis:** Capital, San Luis, alrededores, *Troncoso s.n.* (SI 60286); Belgrano, Alto Pencoso, *Bruch y Carette 24* (SI); Belgrano, Sierra de Las Quijadas, Qda. del Alambre, al W de San Antonio, Ruta Nac. 147, *Hunziker, A. y Cocucci 16388* (CORD). **Santiago del Estero:** La Banda, *Lillo 6082* (LIL); Sarmiento, Reserva forestal de Garza, *Meyer 21829* (LIL); Guazayán, El Cimbolar, *Pierotti s.n.* (LIL). **Tucumán:** Vipos, *Lillo 7894* (LIL); Dpto. Trancas, Tapia, *Venturi 1814* (SI).

13. Justicia glaziovii Lindau, Bull. Herb. Boiss. 3: 483. 1895. TIPO: Brasil. *Glaziou 13073* (lectotipo, designado por Graham (1988), K!).

Rhytiglossa paniculata Nees, in Martius, Fl. Bras. 9: 129. 1847, non *Justicia paniculata* Burm. f. 1768. TIPO: Brasil. Bahia: Ilheos, *Blanchet 2979* (isotipo, BM!).

Lophothecium paniculatum Rizzini, Arq. J. Bot. Rio de Janeiro 8: 336, t. 5. 1948. TIPO: Brasil. Minas Gerais: Ituitaba, *Macedo 1123* (isotipo, BM!).

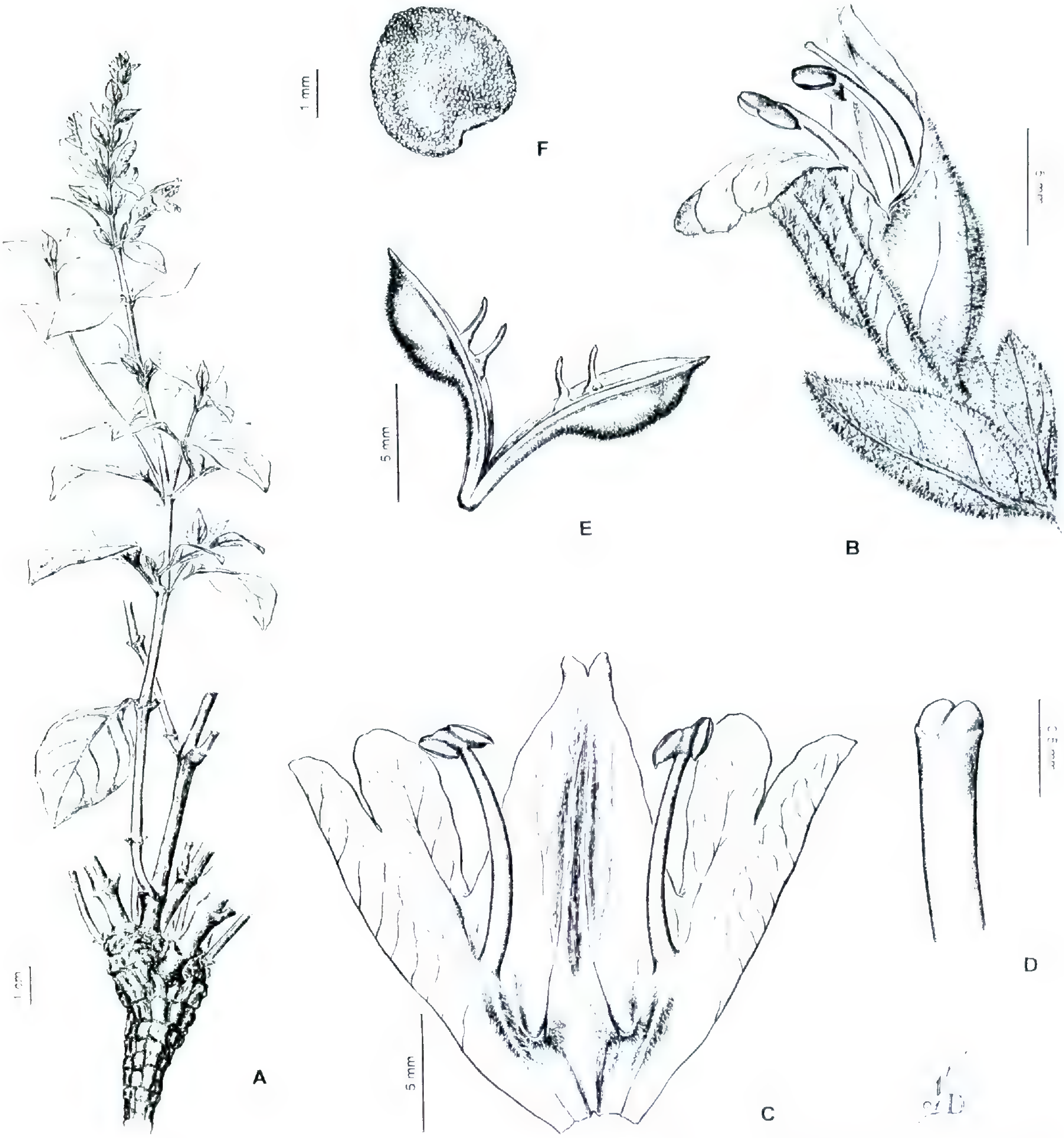

Figura 9. *Justicia gilliesii.* —A. Planta con flores. —B. Flor con bráctea, bractéolas, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. —D. Estilo y estigma. —E. Cápsula abierta. —F. Semilla. *Kiesling 8961* (SI). *Márquez s.n.* (SI 45519).

Justicia velascana Lindau, Bull. Herb. Boiss. 3: 484. 1895. TIPO: Bolivia. "Prov. Velasco orientali", 200 m, Ago., *Kuntze s.n.* (holotipo, B destr., fot. F 8878!; isotipo, NY!).

Arbusto ramoso con tallos ramificados, cilíndricos, cortamente pubérulo-tomentosos. Hojas con pecíolo de 0.5–1.5 cm long., y lámina ovada, de 5–8(–15) cm long. y 2.5–4.5 cm lat. (la de las hojas apicales menor), aguda en el ápice, cuneada a redondeada en la base y algo decurrente sobre el pecíolo, glabra o pubérula en el haz, pubérula o cortamente pubescente en el envés, en especial sobre las venas. Inflorescencias paniculiformes en las axilas de las hojas superiores, amplias, tenues, de espigas laxas reunidas en racimos compuestos generalmente más largos que las hojas, con los raquis pubérulos; brácteas anisofloras, lineales o triangulares, diminutas, de 1–2 mm long. y 0.5 mm lat., glabras o pubérulas; bractéolas similares, más angostas. Cáliz profundamente 5-partido, de ca. 4 mm long., con los segmentos lineales, de 3–4 mm long. por 0.5 mm lat., glanduloso-pubérulos. Corola color crema de 0.8–1.3 cm long., con tubo acampanado de 5–8 mm long. y 3–5 mm diám. en la fauce, los

labios de ca. 5 mm long. el posterior ovado, de 4–5 mm lat., biapiculado, el anterior trilobado, con los lóbulos de ca. 2 mm long. por 2.5 mm lat. Estambres exertos hasta el ápice del lóbulo posterior, con las tecas superpuestas, oblicuas, de menos de 1 mm, separadas por el conectivo, la inferior más pequeña y con un apéndice glandular claviforme en la base. Cápsulas angostamente claviformes de ca. 1 cm long. y 2 mm lat., con el tercio inferior sólido y lateralmente comprimido y la porción superior engrosada, algo estrechada en su parte media, pubérulas. Semillas de 1.5 mm diám., tuberculado-verrugosas; retináculos de ca. 1 mm long.

Ilustraciones. Rizzini, 1948: 339 (sub *Lophotecium paniculatum*).

Distribución, hábitat y fenología. Sur de Brasil, este de Bolivia, y noreste del Paraguay. Habita en bordes de bosque. Florece en verano y otoño, principalmente de enero a marzo.

Justicia glaziovii se caracteriza por las inflorescencias paniculiformes amplias y tenues, con flores color crema de cerca de 1 cm long., y es una especie relativamente rara que ha sido poco coleccionada.

Material seleccionado. PARAGUAY. **Amambay:** in altiplanitie et declivibus "Sierra de Amambay", *Rojas 10864* (BM, G, K, M, NY, P, W); Sierra de Amambay, in via sylvatica, Picada Yatobó, Cerro Porá, *Rojas 10402* (G, NY); Zw. Río Apa und Río Aquidabán, Caballero-Cue, *Fiebrig 4811* (BM, G, K). **Concepción:** Estancia Potrerito, *Basualdo 3485a* (FCQ).

14. Justicia glutinosa (Bremekamp) V. A. W. Graham, Kew Bull. 43: 613. 1988. *Sarotheca glutinosa* Bremek., Proc. Kon. Ned. Akad. Wet. C, 72: 426. 1969. TIPO: Bolivia. *Brooke 5677* (holotipo, BM no visto, fot. US!).

Sarotheca elegans Nees, in Martius, Fl. Bras. 9: 113. 1847, non *Justicia elegans* Beauv. 1810. *Justicia sarotheca* V. A. W. Graham, Kew Bull. 43: 614. 1988. TIPO: Brasil. Goiás: Serra do S. Felis ad Rio Traciras, *Pohl 1989* (holotipo, W!, fot. F 32715!).

Hierba sufruticosa de 0.5–1.5 m alt., con tallos subcilíndricos, largamente hirsuto-pubescentes cuando jóvenes, glabrescentes a la madurez. Hojas con pecíolo de 1–4 cm long., y lámina ovada a anchamente elíptica de 7–15 cm long. por 3–5 cm lat., aguda y acuminada en el ápice, cuneada y decurrente en la base, pubérula en el haz y más o menos hirsuto-pubescente en el envés, especialmente sobre las venas principales. Inflorescencias en espigas densas reunidas en racimos pedunculados en las axilas de las hojas superiores; pedúnculos y raquis glanduloso-pubescentes; brácteas opuestas isofloras o alternadamente anisofloras, lanceoladas, de 2.5–3 mm long. y 1 mm lat., glanduloso-pubescentes; bractéolas lineales, algo menores. Cáliz profundamente 4-partido, con los segmentos lanceolados de 4–6 mm long. y 1.5 mm lat., densamente glanduloso-pubescentes. Corola de ca. 1 cm long., blanca con marcas lilas en la fauce, externamente glanduloso-pubescente, el tubo levemente obcónico, de 4–6 mm long., y labios de 4–5 mm long., el posterior ovado, de 2 mm lat., agudo, el anterior trilobado, con los lóbulos de 1.5–2.5 mm long. redondeados. Estambres exertos hasta el ápice del labio posterior, las anteras con la teca superior oblicua, de ca. 1 mm long., la inferior algo menor y apendiculada en la base. Cápsula claviforme de 1.5–2 cm long. y 0.4 cm diám., densa- y cortamente glanduloso-pubérula. Semillas marcadamente aplanadas, de 3 mm diám., papilosas; retináculos de menos de 2 mm long.

Ilustraciones. Nees, 1847a: tab. 18 (sub *Sarotheca elegans*).

Distribución, hábitat y fenología. Perú, Bolivia, extremo norte de Argentina, sudoeste de Brasil y nordeste de Paraguay. En Paraguay habita en bordes de selvas ribereñas rodeadas de campos cerrados, y florece principalmente en primavera, de agosto a noviembre.

El nombre *Justicia sarotheca* se reduce a la sinonimia de *Justicia glutinosa* por primera vez. Esta especie se caracteriza por sus hojas grandes y flores medianas, de cerca de 1 cm long., en inflorescencias glandulosas de espigas densas reunidas en racimos axilares. Existe una ilustración de esta especie (como *Sarotheca elegans*) en *Flora Brasiliensis* (Nees, 1847a).

Material seleccionado. ARGENTINA. **Salta:** Dep. San Martín, Quebrada Astillero, *Schulz 5484* (CTES). PARAGUAY. **Amambay:** Cerro Corá, en arroyo interrumpido en selva, *Schinini y Bordas 20344* (CTES, G, US); Parque Nacional Cerro Corá, bosque húmedo de hasta 25 m de altura al lado del Arroyo Aquidaban-Ningüí, suelo arenoso, *Brunner 1442* (G, MO); Parque Nacional Cerro Corá, cerca de la casa forestal, en una maleza algo húmeda al lado de la carretera, *Fernández Casas 4114* (G, MO); Parque Nacional Cerro Corá, orilla S del Arroyo Aquidaban-Aguí, *Soria 1727* (FCQ, G, MO); Parque Nacional Cerro Corá, selva marginal de Arroyo Aquidabán-Niguí, Ferrucci, *Vanni y Ferraro 693* (CTES); Parque Nacional Cerro Corá, *Mereles 2054* (G).

15. Justicia goudotii V. A. W. Graham, Kew Bull. 43: 603. 1988. *Chaetothylax umbrosus* Nees, in DC., Prodr. 11: 313. 1847, non *Justicia umbrosa* Benth., Pl. Hartw. 79. 1841. TIPO: Argentina. Tucumán: San Javier, *Tweedie 1262* (lectotipo, aquí designado, K!).

Chaetothylax boliviensis Lindau, Bull. Herb. Boiss. 3: 492. 1895, non *Justicia boliviensis* (Bremek.) V. A. W. Graham, Kew Bull. 43: 613. 1988. TIPO: Bolivia. Santa Cruz: 1000 m, Mayo 1892, *Kuntze s.n.* (sintipo, B destr., fot. F 8897!; isosintipo, NY!); Brasil. Paraná, *s. col. 466* (sintipo, B. destr.).

Chaetothylax vestitus Rizzini, Dusenia 3(3): 191. 1952, non *Justicia vestita* Schult., Mant. 1: 145. 1822. TIPO: Brasil. Paraná: Parque Nacional do Iguazú, 3 Abr. 1949, *Duarte y Pereira 1927* (holotipo, RB no visto).

Hierba perenne, rizomatosa en la base, con tallos erectos subcilíndricos, a veces decumbentes y geniculados, de hasta 80 cm long., pubérulos. Hojas opuestas con pecíolo de 3–10 mm long. y lámina ovada de 2–9 cm long. por 1.5–3.5 cm lat., acuminada en el ápice, cuneada y algo decurrente en la base, entera, pubérula en el haz, pubescente sobre la nervadura en el envés. Inflorescencias formadas por flores sésiles con dos bractéolas en su base, dispuestas en el eje de la inflorescencia formando una espiga unilateral. Espigas terminales o en las axilas de las hojas superiores, a veces enriquecidas por espigas derivadas de yemas supernumerarias. Brácteas y bractéolas lanceoladas, rígidas, de 4–6 mm long., ciliadas, con el nervio medio prominente en el dorso. Cáliz de cerca de 8 mm long., con los 4 segmentos rígidos, lineales, subulados, dorsalmente pubescentes sobre el nervio medio, ciliados. Corola pálido lilacina a violácea de 1.5–2 cm long., con tubo muy angosto de 1–1.5 cm long., estrecho en la garganta, el labio superior erecto, de 4 mm long. por 1 mm lat., el labio inferior ancho, trilobado, de cerca de 5 mm long., con estrías blancas en la fauce. Estambres con filamentos de aprox. 5 mm long.; teca apical perfecta, de contorno ovado, de 1 mm long., la otra inserta más abajo en el filamento, semiestéril, más angosta y basalmente caudada. Cápsula de contorno obovado, de aprox. 7 mm long. por 2.5 mm lat., cortamente sólido-estipitada en la base, glabrescente y de paredes finas. Semillas 4, aplanadas, de 1 mm diám., con pelos cortos y gloquidiados; retináculos de 1 mm long., obtusos.

Ilustraciones. Ezcurra, 1993a: 344.

Distribución, hábitat y fenología. Colombia, Bolivia, Brasil, Paraguay y norte de la Argentina. Habita en el interior o en los bordes de selvas mesófilas y bosques xerófilos de tipo Chaqueño, frecuentemente en ambientes alterados de planicies y serranías hasta 1300 m aprox. Florece a fines de verano otoño e invierno, de enero a julio.

Nombre vulgar. "Uchu yuyo" en el noroeste de Argentina (Burkart, 1943, sub *Chaetothylax umbrosus*).

Esta especie se describió bajo el nombre de *Chaetothylax umbrosus* Nees sobre la base de dos sintipos, uno de Colombia (*Goudot s.n.*, K!) y otro de Argentina (*Tweedie 1262*, K!). Graham le puso un nombre nuevo al pasarla a *Justicia*, *Justicia goudotii* Graham, por ya existir el nombre anterior *Justicia umbrosa* Benth., pero no designó un lectotipo. Debido a que los sintipos pertenecen a dos especies diferentes, una de Colombia y otra de la región subtropical de Sudamérica (norte de Argentina, sudeste de Bolivia, Paraguay y sudoeste de Brasil): (1) Selecciono el ejemplar de Tweedie de Argentina como lectotipo de *Chaetothylax umbrosus* (= *Justicia goudotii*). La elección de este ejemplar se basa en que, ante la falta de otras evidencias en el protólogo, el epíteto *umbrosus* que eligió Nees para la especie coincide con los datos del ejemplar de Tweedie "muy abundante en los bosques mas sombríos de San Javier" (traducido). Por otro lado, la elección de este ejemplar preserva el uso actual del nombre, ya que la especie de la region subtropical de Sudamérica ha sido identificada con los nombres *Chaetothylax umbrosus* y *Justicia goudotii* en varias publicaciones (por ej. Ezcurra, 1993a, 1999), y está identificada con estos nombres en numerosos ejemplares de herbario. (2) El ejemplar de Goudot de Colombia pertenece a la especie determinada por Leonard (1951–1958) como *Chaetothylax huilensis*, que se diferencia de *Justicia goudotii* por las inflorescencias más anchas, las brácteas, bractéolas y lóbulos del cáliz más largos, y las cápsulas mayores.

Material seleccionado. ARGENTINA. **Catamarca:** del Alto, Balcagua, *Venturi 7080* (SI). **Corrientes:** Camino a Sta. Catalina, *Soriano 1685* (SI). **Chaco:** Las Breñas, *Legname y López 8704* (LIL); Sgto. Cabral, PN Chaco, *Múlgura 927* (SI). **Formosa:** Km 39 del FC, *Jörgensen 2338* (SI). **Jujuy:** Sta. Bárbara, Laguna La Brea, *Meyer 8669* (LIL); Ledesma, Sa. Calilegua, *Venturi 5301* (LIL); San Pedro, Sa. Santa Bárbara, *Venturi 9631* (SI). **Salta:** San Martín, de Tartagal a Yacuiba, prox. Ayo. Tobantirenda, *Legname 6857* (LIL); Capital, La Peña, Ruta 51, km 20, 15 km al E de Salta, *Novara 3502* (SI); Anta, Tacuí, 45 Km al S de Macapillo, límite con Santiago, *Novara y Ternel 10284* (LIL); Orán, San Ignacio, *Pierotti 83* (LIL); Rosario de la Frontera, *Venturi 6184* (LIL). **Santa Fe:** Villa Guillermina, *Meyer 2998* (LIL). **Santiago del Estero:** Choya, La Punta, Sa. Del Mogote, Qda. De Calapachín, *Frenguelli 128* (SI); Villa La Punta, Sa. de Guasayán, *Ulibarri 1509* (SI). **Tucumán:** Río Chico, Qda. de Marapa, *Castellanos s.n.* (LIL); Tafí, Parque Aconquija, *de la Sota 1138* (LIL); Tucumán, *Tweedie s.n.* (K); Famaillá, La Fronterita, *Venturi 1724* (SI). PARAGUAY. **Guairá:** Cordillera de Ybytyruzú, Cerro My My, camino a Cerro Polilla, *Zardini y Velásquez 13803* (MO). **Presidente Hayes:** Gran Chaco, Santa Elisa, *Rojas 2818* (BM, G, K, LIL, MO, NY, P); in regione cursus inferioris fluminis Pilcomayo, *Rojas 155* (G); Km 50, *Soria 280* (G); Route Transchaco, pk 320, *Billiet y Jadin 3057* (BM, G, NY).

16. Justicia hassleri (Lindau) V. A. W. Graham, Kew Bull. 43: 615. 1988. *Beloperone hassleri* Lindau, Bull. Herb. Boiss. 6 (App. 1): 30. 1898. TIPO: Paraguay. "In dumeti pr. Itacurubi," *Hassler 1089* (holotipo, G!; isotipos, MO!, NY!, P!).

Chaetochlamys marginata Lindau, Bull. Herb. Boiss. 3: 491. 1895, non *Justicia marginata* Lindau, 1894. *Justicia paraguayensis* V. A. W. Graham, Kew Bull. 43: 615. 1988. TIPO: Paraguay meridional, Sep. 1892, *Kuntze s.n.* (holotipo, B destr., fot. F 8900!; isotipos, G!, NY!).

Hierba sufruticosa, rizomatosa en la base, con tallos erectos subcilíndricos, de hasta 40 cm long., generalmente glabros. Hojas sésiles, opuestas, con lámina ovada de 3.5–6(–9) cm long. por 1.3–3 cm lat., entera, rígida, coriácea, aguda y acuminada en el ápice, redondeada a cordada en la base, con el margen escarioso y las venas prominentes en el envés, glabra. Flores sésiles dispuestas en espigas densas sésiles, terminales o en las axilas de las hojas superiores, con brácteas anisofloras. Brácteas y bractéolas angostamente lanceoladas a lineales, imbricadas, rígidas, de 8–15 mm long. por 1.5–2.5 mm lat., largamente acuminadas, escariosas, con el margen blanquecino. Cáliz 4-partido de 10–15 mm long., con los 4 segmentos rígidos, lineales, subulados, albo-marginados. Corola pálido lilacina a violácea de ca. 2.5 cm long., con tubo muy angosto de 1.5–2 cm long., estrecho en la garganta, el labio superior erecto, de 6 mm long. por 1.5 mm lat., el labio inferior ancho, trilobado, de cerca de 8 mm long., con los lóbulos de 5 mm long. por 4 mm lat., el medio algo mayor. Estambres con filamentos de aprox. 3 mm long.; teca apical perfecta, de contorno ovado, de 1 mm long., la otra inserta más abajo en el filamento, más angosta y basalmente caudada. Cápsula de contorno elíptico, de 6 mm long. y 5 mm grosor, cortamente estipitada en la base, glabra y de paredes finas. Semillas 4, aplanadas, de 1 mm diám., corta y densamente papiloso-pilosas, pardo-oscuras; retináculos agudos.

Ilustraciones. Figura 10.

Distribución, hábitat y fenología. Sur de Brasil (Mato Grosso do Sul) y Paraguay central. Habita en bordes de bosques. Florece a lo largo del año, principalmente en invierno, de junio a septiembre.

Justicia hassleri se asemeja a *J. alopecuroidea* T. F. Daniel (Daniel, 1990), especie de México, lo que sugiere relaciones filogenéticas estrechas entre algunas especies de *Justicia* de Sud y Norteamérica, las que deberían estudiarse.

Material seleccionado. PARAGUAY. **Cordillera:** 3 km desvío ruta 2 a Piribebuy, *Ferrucci 758* (CTES); in dumeto Itacurubi, *Hassler 3053* (G, K, NY, P, W); in dumeto pr. Itacurubi, *Hassler 1138* (G); San Bernardino, orillas montes, *Hassler 138* (SI). **Paraguarí:** Cerrito, in dumetis, *Osten y Rojas 8978* (G); Cerro Hu, pres de Paraguarí, *Balansa 2456* (G, K); Cerro Mbatoví, camino al arroyo Mbatoví, *Basualdo 2658* (FCQ); Cerro Mbatoví, forest along N slope, *Zardini y Velásquez 9943* (MO); Cerro Paraguarí, *Hassler 916* (BM, W), *Fiebrig 916* (E, G, K, M); in regione collium Cerros de Paraguary, *Hassler 6476* (BM, G, K, LIL, NY, W). **S. dep.:** Paraguaria Centralis, *Hassler 3057* (BM); Paraguaria Centralis, reg. lacus Ypacaray, *Hassler 12530* (BM, E, G, LIL, MO, NY, US); Sedparaguay, *Kuntze s.n.* (G).

17. Justicia hunzikeri Ariza Espinar, Kurtziana 6: 92. 1971. TIPO: Argentina. La Rioja: San Martín, Sierra de Ulapes, falda E, frente a Ulapes, 25 Mar. 1958, *Hunziker, A. y Caro 13560* (holotipo, CORD!).

Arbusto de 0.50–1.50 m alt., con ramas erectas, cilíndricas, las jóvenes amarillentas y cuadrisulcadas, con estrías marcadas entre las costillas, generalmente glabras. Hojas cortamente pecioladas, angostamente ovadas a elípticas, de 2–4 cm long. por 0.3–1.5 cm lat., agudas, cuneadas en la base, generalmente glabras, pubérulas solamente sobre la vena media en el envés. Flores sésiles o cortamente pediceladas en espigas terminales y axilares de 3–5 cm. long.; brácteas ovadas o elípticas de 1.4 cm long. por 0.7 cm lat., bractéolas lanceoladas de cerca de 1 cm long. por 0.2 cm lat. Cáliz profundamente 5-partido, con los lóbulos angostamente ovados a lanceolados, subiguales, de 3–4 mm long., foliáceos, generalmente glabros. Corola lilacina de 2–2.5 cm long., pubérula, con tubo corto de cerca de 1 cm long., ensanchado en una garganta de aproximadamente 0.8 cm diám., los labios de 1–1.3 cm long., el anterior trilobado hasta la mitad, con la fauce blanca, convexa y transversalmente rugoso-venosa. Estambres insertos en la base de la garganta, las anteras con las tecas subparalelas, una por encima de la otra, la inferior generalmente apendiculada en la base. Cápsulas obovoides, robustas, glabras, de 0.8–1 cm long. por 5–6 mm diám., con la mitad inferior sólida y lateralmente comprimida. Semillas generalmente 4, suborbiculares, diminutamente rugoso-tuberculadas; retináculos obtusos.

Ilustraciones. Ariza-Espinar, 1971: 93.

Distribución, hábitat y fenología. Endémica de Argentina, se la encuentra en La Rioja, San Juan y San Luis, en regiones áridas. Habita frecuentemente en matorrales serranos sobre suelo rocoso a aprox. 600–800 m s.m. y florece en primavera y verano, de noviembre a marzo.

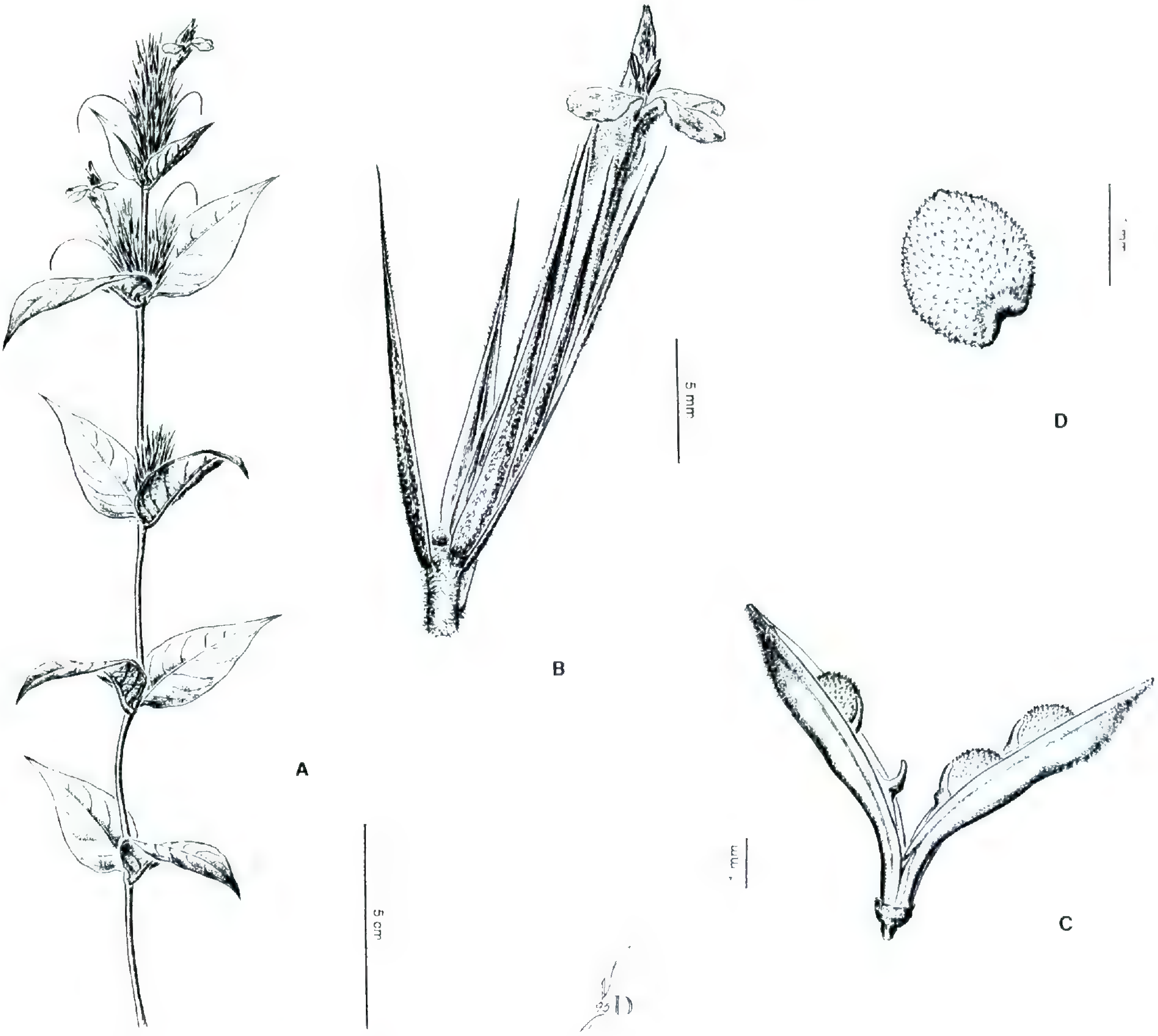

Figura 10. *Justicia hassleri.* —A. Rama con flores. —B. Flor con bráctea, bractéolas, cáliz, corola, estambres y estilo. —C. Cápsula abierta. —D. Semilla. *Hassler 138* (SI).

Justicia hunzikeri se asemeja a *Justicia tweediana* en las corolas lilacinas, pero se diferencia por las flores en espigas secundifloras y las semillas rugoso-tuberculadas sin engrosamiento en el margen, en lo que se asemeja a *Justicia xylosteoides. Justicia hunzikeri* habita un área restringida al extremo NW de San Luis, E de San Juan y S de La Rioja y posee distribución simpátrica con *J. xylosteoides.* Esto sugiere que ambas especies podrían tener un origen filogenético común, pero que actualmente estén aisladas geográficamente y posean diferentes tipos de polinizador.

Material seleccionado. ARGENTINA. **La Rioja:** San Martín, Sierra de Ulapes, falda E, frente a Ulapes, *Hunziker, A. y Caro 13562* (CORD); San Martín, Sierra de Ulapes, Cerro de Minas, *Stuckert 17193* (CORD). **San Juan:** Caucete, cerros al E de Marayes, Ruta 20, *Múlgura 675* (SI); Valle Fértil, Quebrada de Mesada, Chucuma, *Múlgura 738* (SI); Valle Fértil, 3 km al W de Marayes en dirección a San Agustín del Valle Fértil, *Fortunato 5880* (SI); Valle Fértil: de Marayes a Las Tumanas, *Kiesling 3013* (SI). **San Luis:** Belgrano, Sierra del Gigante, cerca de la cantera de Pérez, *Anderson 1936* (CORD); Belgrano, Sierra del Gigante, en las inmediaciones de La Calera, *Hunziker, A. y Maldonado 16245* (CORD).

18. Justicia jujuyensis C. Ezcurra, Bol. Soc. Argent. Bot. 25(3–4): 350. 1988. *Justicia leonardii* De Marco & Ruiz, Publ. Especial Inst. Lillo: 50. 1976, non Wasshausen 1973. TIPO: Argentina. Jujuy: Ledesma, camino al Bananal, antes de llegar a Arroyo Quemado, entrando a la izquierda 3 km, leg. *Legname y Cuezzo 5970C* (holotipo, LIL!).

Hierba sufruticosa de 0.5–1 m alt., con tallos subcilíndricos, cuadrisulcados, pubescentes a casi glabros, con líneas longitudinales pilosas en su juventud. Hojas con pecíolo de 0.5–1.5 cm long. y lámina ovada de 10–16 cm long. por 4–7 cm lat.,

discolor, aguda y acuminada en el ápice, obtusa a redondeada en la base, decurrente sobre el pecíolo, con cistolitos poco notorios en su superficie, generalmente glabra en el envés. Flores sésiles dispuestas en espigas cortamente pedunculadas en las axilas de las hojas superiores. Espigas más cortas que las hojas, densas; brácteas florales lanceoladas, de 8–10 mm long. por ca. 1 mm lat., foliáceas, pubérulas; bractéolas lineal-lanceoladas, de 5–8 mm long. Cáliz 5-partido, de 4–5 mm long., con los segmentos triangulares, de 3–4 mm long., agudos, glabros, ciliados en el margen. Corola blanca de 1.5 cm long., con tubo de 7 mm long. ensanchado en una garganta acampanada de 5 mm diám., y labios de 7–8 mm long., el posterior brevemente bidentado, el anterior ampliamente trilobado erecto, patente. Estambres con filamentos de 6 mm long. y anteras con las tecas a distinta altura, la superior de 2 mm long., la inferior oblicua, algo mayor y con un apéndice glandular en la base. Estilo glabro o pubérulo en la base; estigma bilobado; ovario glabro y disco sinuado. Cápsula de ca. 1 cm long., con la mitad inferior sólida y lateralmente comprimida y la superior subesférica y 4-seminada, de 4 mm diám., glabra o pubérula. Semillas aplanadas, de contorno orbicular, de 3 mm diám., con un reborde en su cara interna; retináculos obtusos, de cerca de 2 mm long.

Ilustraciones. Lillo, 1937, lám. 2 (sub *Justicia nemoralis*). De Marco y Ruiz, 1976: 51, 58 y 59 (sub *J. leonardii*). Ezcurra, 1993a: 357.

Distribución, hábitat y fenología. Sur de Bolivia y norte de la Argentina, en las provincias de Jujuy, Salta, Tucumán y Santiago del Estero. Habita en lugares húmedos y sombreados de bosques de transición en la zona de contacto entre las provincias fitogeográficas Chaqueña y de las Yungas. Florece en verano, de enero a marzo.

Nombre vulgar. "Ichiyuyo" (Ezcurra, 1993a).

Justicia jujuyensis se asemeja mucho a *J. corumbensis*, pero habita una región más occidental y se diferencia por las inflorescencias cortamente pedunculadas más cortas que las hojas. Los nombres *Justicia nemoralis* Lillo y *Justicia nemoralis* Lillo var. *tomentosa* Lillo (Lillo, 1937) son nomina nuda que fueron utilizados ampliamente para esta especie en etiquetas de herbario. El nombre *Justicia nemoralis* S. Moore (J. Bot. 47: 296. 1909) utilizado para una especie de África es un homónimo anterior que no permite su utilización para la especie de América del Sur. Por esta razón se creó el nombre nuevo *Justicia jujuyensis* para esta especie (Ezcurra, 1988).

Material seleccionado. ARGENTINA. **Jujuy:** Santa Bárbara, Palma Sola a El Fuerte, ca. 5 km, *Kiesling 5562* (SI); Ledesma, Calilegua, toma del Arroyo del Medio, *Cabrera 31312* (SI); Valle Grande, Ledesma a Valle Grande, *Meyer 16416* (LIL). **Salta:** Orán, Vespucio, camino a la Cruz, *Abbiatti y Claps 221* (LIL); Metán, Metán frente al pueblo, 2 km W de la ruta 9/34, *Novara 5826* (M, SI); Rosario de la Frontera, El Naranjo, *O'Donnell 5368* (LIL); Rosario de Lerma, Campo Quijano, *Venturi 8121* (K, SI). **Santiago del Estero:** C. Pellegrini, C° del Remate, *Venturi 5853* (K, SI). **Tucumán:** Trancas, Qda. de la Huiguera, *de la Sota 96* (LIL); Famaillá, Qda. de Lules, Río Lules, *Herrera 232* (LIL); Tafí del Valle, Yerba Buena, *Venturi 88* (SI); Burruyacu, El Timbó, *Venturi 2835* (LIL).

19. Justicia kuntzei Lindau, Bull. Herb. Boiss. 3: 483. 1895. TIPO: Bolivia. Santa Cruz: 1000 m, V 1892, *Kuntze s.n.* (B destr.; isotipo, NY!).

Lophothecium boliviense Bremek., Verh. Kon. Ned. Akad. Wetensch. Afd. Naturk., Tweede sect. C, 72(4): 426. 1969. TIPO: Bolivia. Camiri: on Rio Parapeti oil refinement and commencement of the pipeline, 2500 ft., 4 Sep. 1949, *Brooke 5586* (holotipo, BM!; isotipo, NY!).

Sufrútice o arbusto de hasta 1 m alt. con ramas cilíndricas, lisas, pubérulas en su juventud, glabrescentes y engrosadas por encima de los nudos a la madurez. Hojas con pecíolo de hasta 1.5 cm long. y lámina elíptica de 6–12 cm long. por 2.5–5 cm lat. (la de las hojas apicales menor), aguda o acuminada en el ápice, cuneada y decurrente en la base, esparcidamente pubérula en el haz y sobre la nervadura en el envés. Flores sésiles, con 2 bractéolas en la base, en las axilas de brácteas lineales y pequeñas, agrupadas en espigas laterales reunidas en racimos simples o compuestos, laxos, paniculiformes, generalmente axilares y más largos que las hojas. Brácteas de las flores de 1.5–2.5 mm long.; bractéolas menores. Cáliz de 3–4 mm long. con los 5 segmentos lineales, agudos, glabros. Corola lilacina manchada de blanco en la fauce, de 1.5–2 cm long., con tubo basal de 3–4 mm long., garganta obcónica e inflada de 5 mm long. por 4 mm diám., labio posterior entero, de 10–12 mm long. por 6–8 mm lat., el anterior trilobado, de 8–10 mm long. por 5–6 mm lat., con lóbulos de cerca de 1 mm long. por 2 mm lat. Filamentos de 10 mm long.; anteras con las tecas superpuestas, separadas por el conectivo de 1 mm long., la teca inferior basalmente apendiculada, con un apéndice glandular claviforme de 0.5 mm long. Estilo glabro; estigma levemente engrosado; disco sinuado. Cápsulas de 1.5 cm long. por 3–4 mm diám. con la mitad inferior sólida y lateralmente comprimida y la superior engrosada, de contorno oblongo, estrechada en su parte media. Semillas 4 o menos por aborto,

orbiculares, oscuras, de 1.5–2 mm diám., tuberculadas.

Ilustraciones. Ezcurra, 1993a: 355.

Distribución, hábitat y fenología. Bolivia y N de la Argentina, donde habita en el sotobosque de la selva en serranías de 600 a 1500 m de elevación. Florece principalmente en primavera, de agosto a noviembre.

Justicia kuntzei se caracteriza por las hojas grandes y las inflorescencias multifloras de flores medianas con corola lilacina manchada de blanco en la fauce.

Material seleccionado. ARGENTINA. **Jujuy:** Ledesma, Sa. Calilegua, bajo bosque alto, *Venturi 5217* (SI, K); Capital, Zapla, *Burkart 30640* (SI); Ledesma, 10 km NE of Ledesma, *Eyerdam y Beetle 22275* (SI, K). **Salta:** Santa Victoria, PN Baritú, Arroyo Sidras, *Brown 2007* (SI); Anta, PN El Rey, camino a Pozo Verde, *Novara y Charpin 10344* (LIL); Santa Victoria, camino de Baritú a Porongal, *Marmol 8734* (LIL); Orán, Tartagal, *Schreiter 11370* (SI); San Martín, Dique Itiyuro, *Stange s.n.* (LIL).

20. Justicia laevilinguis (Nees) Lindau, Engler Bot. Jahrb. 19, Beibl. 48: 20. 1894. *Rhytiglossa laevilinguis* Nees, in Martius, Fl. Bras. 9: 120. 1847. *Dianthera laevilinguis* (Nees) Durand & Jackson, Ind. Kew. Suppl. 1: 132. 1902. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, *Sellow s.n.* (sintipo, B destr.); San Gabriel, Estancia dos Fideles, *Sellow s.n.* (sintipo, B destr.); sin loc., *Sellow s.n.* (probables isosintipos, K!, E!); Isla Santa Catarina, *Tweedie s.n.* (sintipo, K no visto); Argentina. Córdoba: Río Segundo, *Tweedie s.n.* (sintipo, K!).

Rhytiglossa laevilinguis Nees var. *longifolia* Nees, in Martius, Fl. Bras. 9: 120. 1847. TIPO: Argentina. Buenos Aires: *Bacle s.n.* (holotipo, G herb. DC no visto, microficha!; probable isotipo, K!).

Rhytiglossa anagallis Nees, in Martius, Fl. Bras. 9: 119. 1847. *Justicia anagallis* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4(3B): 351. 1895. TIPO: Brasil. Bahia: Caitaité et Caxoeira, *Martius s.n.* (sintipo, M!); entre Porto Alegre y Montevideo, *Sellow s.n.* (sintipo, B destr., fot. F 8808!); Uruguay. San José, *Sellow s.n.* (sintipo, B destr.).

Rhytiglossa repens Nees, in Martius, Fl. Bras. 9: 119. 1847. *Justicia repens* (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4, Abt. 3b: 351. 1895. TIPO: Brasil. *Sellow s.n.* (holotipo, B destr., fot. F 8862!).

Rhytiglossa obtusifolia Nees, in Martius, Fl. Bras. 9: 120. 1847. *Justicia obtusifolia* (Nees) Lindau, Bull. Herb. Boiss. Ser. 2, 3: 663. 1903. TIPO: Brasil. Rio Grande do Sul: Porto Alegre, *Sellow s.n.* (sintipo, B destr.); Argentina. Buenos Aires, herb. *Arnott s.n.* (sintipo, E!).

Rhytiglossa obtusifolia Nees var. *hirsuticaulis* Nees, in Martius, Fl. Bras. 9: 120. TIPO: Brasil. Río Negro, *Riedel s.n.* (holotipo, LE no visto).

Dianthera paludosa S. Moore, Trans. Linn. Soc. 2, Bot. 4: 432. 1895. *Justicia paludosa* (S. Moore) V. A. W. Graham, Kew Bull. 43(4): 600. 1988. TIPO: Brasil. *Moore 941* (holotipo, BM!; isotipos, NY!, B destr., fot. F 8850!).

Dianthera graminifolia Rusby, Mem. New York Bot. Gard. 7: 366. 1927. TIPO: Bolivia. *Rusby 1421* (holotipo, NY!).

Justicia ascendens Bridarolli, Not. Mus. La Plata 13, Bot. 12: 92. 1948. TIPO: Argentina. Buenos Aires: Tigre, *Lanfranchi 300* (holotipo, LP no visto).

Hierba palustre, con rizomas horizontales gruesos y tallos ascendentes, simples o ramosos, radicantes en los nudos inferiores, subtetrágonos, cuadrisulcados, de hasta 80 cm alt. y 5 mm diám., glabros, a veces algo pubescentes. Hojas superiores sésiles, las inferiores con pecíolo de hasta 3 mm long., oblongas a lanceoladas, a veces lineales, de 3–12 cm long. y (0.2–)0.5–1.5(–2.5) cm lat., obtusas en el ápice, redondeadas en la base, enteras o levemente crenadas, generalmente glabras. Flores en espigas unilaterales terminales o axilares de 5–12 cm long., con pedúnculos de hasta 8 cm long. y entrenudos de ca. 1 cm long.; brácteas triangulares de 1.5–3 mm long. por ca. 1 mm lat., y bractéolas triangular-lanceoladas de 1 mm long., ambas glabras. Cáliz 5-partido con segmentos lineal-lanceolados de hasta 1 mm long. y 0.25 mm lat., agudos. Corola lilacina, de 1.5–2 cm long. con tubo basal de 6–10 mm long. por 3 mm diám., más ancha en la garganta; labio posterior ovado, de ca. 1 cm long. y ca. 4 mm lat., obtuso a bidentado, y labio inferior de 13 mm long., trilobado, con los lóbulos de 6 mm long. y ca. 5 mm lat., el del medio algo más ancho y con dibujo pectinado-rugoso y con manchas en la fauce. Estambres exertos, inclusos debajo del labio posterior, con las anteras superpuestas de menos de 2 mm long., separadas por el conectivo. Cápsula de ca. 2 cm long. y 6 mm lat., estipitada, muy aplanada en la porción superior, apiculada y glabra. Retináculos de ca. 3 mm long., bidentados. Semilla suborbicular, de ca. 5 mm diám., muy aplanada, glabra, con el margen delgado y lacerado.

Ilustraciones. Dawson, 1979: 575.

Distribución, hábitat y fenología. Colombia, Venezuela, Perú, Bolivia, sur de Brasil, Uruguay, noreste de Argentina y Paraguay. Habita en ambientes palustres de regiones bajas. En el sur de su distribución florece en primavera y verano, de octubre a abril.

Justicia laevilinguis es una especie higrófila muy variable en su morfología, con una distribución muy amplia en América del Sur. Presenta especies estrechamente relacionadas en América del Norte

como *Justicia ovata* (Walter) Lindau, que se asemeja en la morfología de tallo, inflorescencia y flor, y cuyas relaciones deberían estudiarse.

Material seleccionado. ARGENTINA. **Buenos Aires:** Ribera argentina del Río de la Plata, *Hicken 12911* (SI); La Plata, *Tweedie s.n.* (K, SI). **Corrientes:** Saladas, *Arbo y Tur 2214* (LIL); San Luis del Palmar, Ayo. Riachuelito, 25 Km E de San Luis del Palmar, *Quarín 367* (LIL); Concepción, *Ybarrola 324* (LIL); Gral. Paz, Gral. Paz, *Ybarrola 3504* (LIL); Ituzaingó, RN 12, 20 km de Ituzaingó hacia el E, *Zuloaga 3230* (SI). **Chaco:** Las Palmas, *Jörgensen 2335* (LIL); Resistencia, Margarita Belén, *Meyer 3797* (LIL); Puente de la Plaga, PN Chaco, Pajonal, *Múlgura 1039* (SI). **Entre Ríos:** Uruguay, Concepción del Uruguay, Arroyo La China, campos vecinos, *Bacigalupo 1376* (SI); Gualeguaychú, Gualeguaychú, *Meyer 10281* (LIL). **Formosa:** Pilcomayo, Estancia Bouvier, riacho Araguay, *Guaglianone 454* (SI); Pirané, Pirané, *Morel 161* (LIL). **Misiones:** Posadas, riberas del río, campos, *Bertoni 1168* (LIL); Candelaria, Pindapoy, *Bertoni 2433* (LIL). **Santa Fé:** Gral. Obligado, Villa Ana, *Hayward 1444* (LIL); San Jerónimo, Riacho Coronda, frente a Pto. Gaboto, *Morello 16936* (SI); Las Colonias, Esperanza, *Ruiz Huidobro 3250* (LIL); Garay, Santa Rosa, *Ruiz Huidobro 3348* (LIL). PARAGUAY. **Alto Paraguay:** Alto Paraguay, Chaco, *Fiebrig 1269* (K, M); Puerto Casado (Chaco), *Rojas 2199* (SI). **Amambay:** in palude in regione cursus superoris fluminis Apa, *Hassler 8160* (K, W), *8160a* (BM, G, NY, P); in regione cursus superioris fluminis Apa, *Hassler 8160a* (BM, G, NY). **Caaguazú:** cerca y al Sur de Yhú, junto al arroyo Yhú, *Fernández Casas et al. 7516* (G, MO, NY). **Canindeyú:** in regione vicine Igatimí, in regione Yerbalium de Maracayú, *Hassler 4889* (BM, G, NY, P, W). **Central:** L'Assumption, sur le bord des marads, *Balansa 2449* (G, P); Margen S del río Salado, camino de Limpio a Emboscada, *Arbo et al. 1657* (CTES, US); Patino, near Asunción, *Teague 572* (BM). **Concepción:** Pr. Concepción, *Hassler 7624* (BM, G, NY), *Hassler 7560* (BM, G, K, MO, NY, P); Zw. río Apa und río Aquidabán Centurión, *Fiebrig 4030* (BM, E, G, K). **Cordillera:** Cordillera de Altos, *Fiebrig 356* (BM, E, K, M, US, W); Cordillera de Altos, in campis, *Hassler 3508* (BM, G, K, NY, P, W); Cordillère de Peribebuy, dans les pâturages humides, *Balansa 2451a* (G, P); San Bernardino, costa del Lago Ipacaray, *Quarín et al. 1510* (CTES, US); Tobaty, Arroyo Tobaty, *Archer y Rojas 4847* (US). **Guairá:** on meadows, Villarica, *Jörgensen 4237* (K, MO, NY, US); Villa Rica, *Balansa 2451* (G, K, P). **Ñeembucú:** Pilar, Frente a la boca del río Bermejo, *Meyer 16102* (LIL). **Paraguarí:** Loma Acahay, s.f., *Chodat s.n.* (G); Caballero, *Morong 435* (NY); Cerro Mbatobí, forest along N slope, in regeneration, *Zardini y Velásquez 9935* (BM). **Presidente Hayes:** Estero Patiño, km 164 de la ruta Trans Chaco, *Schinini y Palacios 25919* (CTES, G); Pilcomayo River, *Morong 1031* (BM, K, NY, US); Ruta Trans Chaco, km 78, *Mereles 2430* (CTES, G). **San Pedro:** in regione vicine San Estanislao, *Hassler 5984* (BM, G, K, P, NY, W); San Estanislao, Río Tapiracuay, *Krapovickas et al. 13896* (CTES, US). **S. dep.:** ad ripam occidentalem flum. Paraguay, Gran Chaco, *Rojas 2930* (G).

21. Justicia lilloana Ariza Espinar, Kurtziana 6: 84. 1971. TIPO: Argentina. San Juan: Valle Fértil, campo de Ischialasta, 17 Ene. 1907, *Kurtz 14223* (holotipo, CORD!).

Arbusto bajo, de hasta 0.50 m alt., con ramas erectas, cilíndricas, las jóvenes verdosas y tetrágonas y cuadrisulcadas, con estrías marcadas entre las costillas, pubescentes en los nudos, de corteza cenicienta a la madurez. Hojas cortamente pecioladas, angostamente ovadas a elípticas, de 0.5–1.5 cm long. por 0.3–0.5 cm lat., obtusas, cuneadas en la base, generalmente pubescentes. Flores sésiles o cortamente pediceladas, con dos bractéolas en la base, solitarias en las axilas de brácteas, formando en conjunto espigas laxas; bractéolas lanceoladas de cerca de 1 cm long. por 2 mm lat.; brácteas obovadas de ca. 9 mm long. por 4 mm lat., ambas glandulosas y ciliadas. Cáliz profundamente 5-partido, con los lóbulos angostamente ovados a lanceolados, subiguales, de 4 mm long., foliáceos, generalmente glabros. Corola azul violáceo, lilacina a blanca de 2 cm long., pubérula, con tubo corto de cerca de 1 cm long., ensanchado en una garganta de aproximadamente 0.8 cm diám., los labios de 1–1.3 cm long., el anterior trilobado hasta la mitad, con la fauce blanca, convexa y transversalmente rugoso-venosa. Estambres insertos en la base de la garganta, las anteras con las tecas subparalelas, una por encima de la otra, la inferior generalmente apendiculada en la base. Cápsulas claviformes, muy fuertemente comprimidas, de 1.1–1.5 cm long. por 5–7 mm ancho, glabras y de brillo nacarado en su superficie, con el cuarto inferior sólido y lateralmente comprimido. Semillas generalmente 4, suborbiculares, aplanadas, de 6–7 mm diám., lisas; retináculos obtusos.

Ilustraciones. Ariza-Espinar, 1971: 85.

Distribución, hábitat y fenología. Noroeste de la Argentina, desde Salta, Tucumán y Catamarca hasta La Rioja y San Juan. Se la encuentra en regiones áridas entre 1300 y 2600 m s.m., en montes xerófilos bajos, sobre suelo rocoso. Florece en verano, de diciembre a abril.

Nombre vulgar. "Alfalfillo" (Ariza-Espinar, 1971).

Justicia lilloana se caracteriza por sus hojas pequeñas y sus inflorescencias glandulosas, sus cápsulas grandes y muy fuertemente comprimidas de superficie glabra y brillo nacarado, y sus semillas anchas, muy aplanadas y lisas. El nombre *Justicia platicarpa* Lillo es un nomen nudum que se utilizó para esta especie (Lillo, 1937).

Material seleccionado. ARGENTINA. **Catamarca:** Belén, Los Nacimientos, *Cabrera 16761* (CORD). **La Rioja:** Gral. Lavalle, Parque de Talampaya, *Hunziker, J. y Gamerro 11669* (SI); Independencia, entre Pagancillo y El Balde (ruta Villa Unión a Patquía, km 96/97), *Hunziker, A. 22441* (SI); Independencia, entre Puerta de Talampaya

y Gualo, *Kurtz 13260* (CORD). **San Juan:** Ischigualasto, *Roig 8053* (CORD); Iglesia, Cuesta del C° Negro, entre Talasto y Las Coloradas, *Ruiz Leal 22103* (LIL). **Tucumán:** Tafí, Amaicha, *Diers 225* (SI); Trancas, Lomas de Las Areas, *Schreiter 1105* (CORD, LIL).

22. Justicia lilloi (J. L. Lotti) C. Ezcurra, in Cabrera, Fl. Prov. Jujuy (República Argentina) 9: 349. 1993. *Chaetochlamys lilloi* J. L. Lotti, Publ. Especial Inst. Lillo: 63, fig. 1 y lám. 1. 1976. TIPO: Argentina. Salta: Capital, 600 m s.m., *Lillo 8087* (holotipo, LIL!).

Hierba sufruticosa, de 0.50–1.50 m alt., con tallos subcilíndricos, cuadrisulcados, erectos, pubérulos. Hojas con pecíolo de 0.5–2 cm long. y lámina ovada o elíptica de 5–9 cm long. por 2–4 cm lat., aguda en el ápice y cuneada o redondeada en la base, verde clara, pubérula, con cistolitos densamente esparcidos en su superficie, las venas principales prominentes en el envés. Flores sésiles en dicasios condensados y generalmente reducidos a una flor con dos bractéolas, agrupados en cortas espigas con brácteas foliosas. Espigas axilares y terminales, con el pedúnculo corto y el raquis reducido a uno o dos entrenudos; brácteas muy similares a las hojas, pero sésiles y algo menores, y truncadas o cordadas en la base; bractéolas lineales, de hasta 15 mm long., pubescentes y cortamente ciliadas. Cáliz profundamente 5-partido, con los segmentos ovado-lanceolados, rígidos, de 10–12 mm long. por 2–3 mm lat., acuminados y densa y cortamente ciliados, con el nervio medio prominente en el envés. Corola lilacina de 3–4 cm long., con el tubo de 2 cm long. por 3–4 mm diám., poco ensanchado en la garganta, los labios de cerca de 1.5 cm long., el posterior de 7 mm lat., bidentado, el anterior profundamente trilobado, con los lóbulos de 1.2 cm long. por 6–8 mm lat. Estambres con filamentos de 12 mm long. y anteras con las tecas superpuestas y algo separadas por el conectivo, la superior de 2.5 mm long., la inferior de 3 mm long. y apendiculada en la base. Estilo glabro con estigma levemente engrosado y bilobado; ovario glabro y disco en forma de copa, ondulado. Cápsulas de cerca de 1.5 cm long. y 6 mm diám. con la mitad inferior sólida y lateralmente comprimida y la superior engrosada, ovoide y 4-seminada. Semillas orbiculares subesféricas, de 2–3 mm diám., lisas, pardo-oscuras; retináculos de 3 mm long.

Ilustraciones. Lillo, 1937: lám. 7 y 8 (2) (sub *Chaetochlamys tucumanensis*). Ezcurra, 1993a: 350.

Distribución, hábitat y fenología. Sudeste de Bolivia, oeste de Paraguay y norte de la Argentina. Habita principalmente en facies húmedas y bajas del Chaco Serrano septentrional y en bosques de transición a las selvas montanas de las Yungas entre 500 y 1200 m de elevación. También se encuentra en laderas de cerros del Chaco Paraguayo. Florece de fines de primavera a otoño, de diciembre a mayo.

Chaetochlamys tucumanensis Lillo es un nomen nudum con el que originalmente se denominó a esta especie (Lillo, 1937; Lotti, 1976). *Justicia lilloi* es una especie muy afín a *Justicia thunbergioides* (Lindau) Leonard, descripta para Mato Grosso do Sul, Brasil (Brasil. Mato Grosso pr. Corumba, *Malme 3026*, sintipo B destr., fot. F 8949!), y los límites entre ambas no son claros (Ezcurra, 1993b). Junto con *Justicia allocota* Leonard (Brasil. Goiás: *Yale Dawson 15023*, holotipo, US!) y *Justicia venusta* (Rizzini) V. A. W. Graham (Brasil. Minas Gerais: *Brade 17563*, isotipo, US!) forman un grupo de diferenciación compleja que parecen todas derivadas de un antecesor común y adaptadas a diferentes regiones con distintas condiciones de humedad y precipitación. *Justicia lilloi* es la que presenta generalmente hojas más chicas y se encuentra principalmente en las selvas pedemontanas de las Yungas de Bolivia y Argentina y en serranías del Chaco Paraguayo, mientras que *Justicia thunbergioides* y *Justicia allocota* se encuentran en regiones más húmedas del sudoeste y centro de Brasil respectivamente.

Material seleccionado. ARGENTINA. **Catamarca:** El Alto, entre Alijilán y El Alto, *Cristóbal 340* (LIL). **Jujuy:** Santa Bárbara, Abra de los Morteros, *Cabrera 21719* (SI); San Pedro, de San Pedro a El Milagro entrando hacia el este, *Legname 5372* (LIL). **Salta:** Rosario de la Frontera, *Lillo 4417* (LIL); Dpto. La Viña, OSMA, ruta 68, km 163, Lomas al N del puente sobre el Arroyo, Chaco serrano seco, *Novara 8532* (SI); Orán, Cerro Tartagal, *Pierotti 7172* (LIL); Metán, Metán, *Rocha 108* (LIL); Capital, La Lagunilla, *Saravia Toledo 2138* (SI). **Tucumán:** Trancas, aprox. 200 m antes de Vipos, *Vervoorst 4221* (SI); Capital, Barranca Colorada, *Venturi 1150* (SI); Cruz Alta, Barranca de la finca Guillermina, *Schreiter 4492* (LIL); Burruyacu, camino a Cerro Medina, *Villa Carenzo 1750* (LIL). PARAGUAY. **Alto Paraguay:** Cerro Pedrera, Río Navileque, Fuerte Olimpo, *Bernardi 20425* (G); Fuerte Olimpo, Chaco Paraguayo, *Rojas 13842* (LIL); Fuerte Olimpo, in collinis Tres Marías, Alto Paraguay, *Bernardi 20335* (G, MO). **Chaco:** Chaco, Cerro León, desde lomada al S (campamento) hasta meseta Central, *Charpin y Ramella 21733 p.p.* (G). **S. dep.:** Paraguay, *Weddel 3117* (P).

23. Justicia lythroides (Nees) V. A. W. Graham, Kew Bull. 43: 603. 1988. *Heinzelia lythroides* Nees, in Martius, Fl. Bras. 9: 154. 1847. TIPO: Brasil. Rio de Janeiro: "ad fluvium Pirahy," *Pohl s.n.* (holotipo, W!).

Heinzelia ovalis Nees, in Martius, Fl. Bras. 9: 154. 1847.

non *Justicia ovalis* Ridley, J. Fed. Malay States Mus. 10: 150. 1820. TIPO: Brasil. São Paulo: São Paulo, Ypanema, III 1834, *Riedel 1983* (lectotipo, aquí designado, LE, fotogr. US!).

Hierba perenne, rizomatosa en la base, con tallos tenues, subcilíndricos, decumbentes y geniculados, luego erectos, de hasta 40(–70) cm long., pubérulos. Hojas opuestas con pecíolo de 3–10 mm long., y lámina elíptica a angostamente ovada de 3–8 cm long. por 1.3–3 cm lat., aguda o acuminada en el ápice, cuneada y algo decurrente en la base, entera, generalmente glabra, a veces pubérula sobre el nervio medio en el haz, verde clara y pubescente sobre la nervadura en el envés. Inflorescencias formadas por flores en espigas unilaterales tenues, simples o compuestas y ramificadas, de 4–8 cm long., terminales o en las axilas de las hojas superiores, cortamente pedunculadas, con el eje arquado. Brácteas y bractéolas lineal-lanceoladas, rígidas, de 1–3 mm long., pubérulas, con el nervio medio prominente en el dorso. Cáliz de cerca de 6 mm long., con los 4 segmentos de 5 mm long., rígidos, lineales, subulados, dorsalmente pubescentes sobre el nervio medio. Corola blanca, pálido lilacina o violácea de ca. 1 cm long., con tubo de 0.5–0.6 cm long. por 1.5 mm diám., ampliado en la garganta, el labio superior erecto, lanceolado, de 3 mm long., agudo, el inferior ancho, trilobado, de ca. 4 mm long., con los lóbulos de ca. 2 mm long., redondeados. Estambres con filamentos de aprox. 4 mm long.; teca apical perfecta, de 1 mm long., la inferior estéril, reducida a un leve engrosamiento sobre el filamento. Cápsula de contorno angostamente elíptico, de aprox. 5 mm long. por 1.5 mm lat., cortamente sólido-estipitada en la base, glabrescente y de paredes finas. Semillas 4, algo aplanadas, de 1 mm diám., pardo-oscuras, con pelos cortos y gloquidiados; retináculos de 1 mm long., obtusos.

Ilustraciones. Nees, 1847a: tab. 97. Ezcurra y Acosta-Castellanos, 1997: 108.

Distribución, hábitat y fenología. Sur de Brasil, noreste de Argentina y Paraguay oriental. Habita en el sotobosque y en bordes de bosques húmedos, frecuentemente en lugares alterados. Florece en otoño e invierno, de abril a agosto.

Justicia lythroides se caractriza por sus flores en espigas secundifloras tenues y delicadas y sus flores pequeñas. Es muy afín a la especie descripta bajo el nombre de *Chaetothylax hatsbachii* Leonard (Brasil. Paraná: Cerro Azul, Turvo, Rio Ribeira, *Hatschbach 5419*, holotipo US!), que podría ser sinónimo de esta especie.

El nombre *Heinzelia ovalis* fue creado por Nees sobre la base de tres ejemplares: dos de Brasil (São Paulo, Ipanema, *Riedel 1983*, y Minas Gerais, Barbacena, *Riedel 88*, LE) y uno de Argentina, Tucumán (*Tweedie s.n.*, K!). Estos sintipos comprenden una mezcla de dos especies. El ejemplar coleccionado en Argentina por Tweedie pertenece a *Justicia goudotii*, mientras que el material de Brasil coleccionado por Riedel, del que he visto una fotografía y un probable isosintipo (Brasil. São Paulo, in sylvula ad vias pr. Ypanema, III-1834, *Riedel s.n.*, NY!) pertenece a *Justicia lythroides*. Debido a que la diagnosis de *Heinzelia ovalis* coincide más con las características del material de Riedel que con el de Tweedie en tamaño de hojas y flores, designo como lectotipo de *Heinzelia ovalis* al ejemplar de *Justicia lythroides* de Brasil, Ipanema, *Riedel 1983* (LE). Esta designación hace que el nombre *Heinzelia ovalis* deba considerarse sinónimo de *Justicia lythroides*.

Material seleccionado. ARGENTINA. **Misiones:** Eldorado, Eldorado, km 28, *Burkart 14603* (SI); Frontera, reforestación Gral. Manuel Belgrano, *Cuezzo y de la Sota 1527* (LIL); Iguazú, Pto. Libertad, Salto Uruguay, *Fernández 144* (CTES); Cainguás, Arroyo Caña-Pirú, 8 km de A. del Valle hacia Jardín de América, *Hunziker, J. 10891* (SI); San Ignacio, Ayo. Macaco, *Schwarz 5687* (LIL); Montecarlo, Colonia Monte Carlo, *Porta 39* (SI); Iguazú, Salto Urugua-í, *Zuloaga 2188* (SI). PARAGUAY. **Alto Paraná:** Alto Paraná, *Fiebrig 6040* (G); in regione fluminis Alto Parana, *Fiebrig 6173* (G, SI); Río Itabó, sotobosque, ribera del río, *Itaipú Binacional 1001* (MO). **Caazapá:** Tavaí, Castor Cue, 26°10′S, 55°20′W, *Degen 1611* (MO); Tavaí, Compañía Toranzos, *Degen 1522* (G, MO), *Ortiz 1280* (G, MO). **Canindeyú:** Mbaracayú, comunidad Mbyá, *Basualado 2546* (FCQ).

24. Justicia mandoni (Lindau) Wasshausen & C. Ezcurra, Candollea 52: 175. 1997. *Beloperone mandoni* Lindau, Bull. Herb. Boiss. 5: 675. 1897. TIPO: Bolivia. La Paz: Larecaja, in vicinity of Sorata, Cerro Iminapi, *Mandon 297* (holotipo, B destr.; isotipos, BM! p.p., K! p.p.).

Justicia odonellii De Marco & Ruiz, Publ. Espec. Inst. Lillo: 53, fig. 3 y láms. 5 y 6, 1976. TIPO: Argentina. Tucumán: Chicligasta, Puesto Las Pavas, 1060 m s.m., *Meyer 15125* (holotipo, LIL!).

Sufrútice o arbusto apoyante de 1–2 m alt., con ramas cilíndricas, lisas o muy finamente estriadas, generalmente glabras. Hojas con pecíolo de 0.5–1 cm long., pubérulo, y lámina angostamente ovada, de 4–8 cm long. por 1.2–2.5 cm lat., redondeada y levemente decurrente en la base, acuminada en el ápice, levemente pubescente en el envés, pubérula en el haz, con nervaduras marcadas. Flores sésiles con dos bractéolas basales en las axilas de brácteas dispuestas en espigas generalmente terminales, las brácteas opuestas pero alternadamente anisofloras, dándole un aspecto unilateral a la espiga. Brácteas

elíptico-lanceoladas, de 1–1.5 cm long. por 1.5–2.5 mm lat., foliosas, pubescentes; bractéolas lineal-lanceoladas, de 1–2 mm lat., algo más cortas que el cáliz. Cáliz profundamente 5-partido, los segmentos subiguales, ovado-lanceolados, de 1.5–2 cm long. por 2–3 mm lat., generalmente glabros a pubérulos. Corola rojo-morada de 3–3.5 cm long., el tubo de aprox. la misma longitud que los labios y de 5 mm diám., interiormente surcado en la parte posterior por dos pliegues longitudinales que alojan el estilo, el labio posterior bidentado, de 1.5–2 cm long. por aprox. 8 mm lat., el anterior trilobado, de 7 mm lat., reticulado-venoso y convexo en la base, con los lóbulos de aprox. 1 cm long. por 3–4 mm lat. Estambres con filamentos de 2 cm long. y tecas situadas a distinta altura, la superior de 2 mm long., mútica, la inferior separada del conectivo, algo más grande y apendiculada en la base. Cápsula de contorno oblongo, de 1.5–2 cm long. por 0.5 cm diám., pubescente, estipitada. Semillas aplanadas de 2 mm diám., verrugosas; retináculos de 2 mm long.

Ilustraciones. Lillo, 1937: lám. 6 (sub *Justicia tucumanensis*). De Marco y Ruiz, 1976: 54, 60 y 61 (sub *Justicia odonellii*). Ezcurra, 1993a: 337 (sub *Justicia odonellii*).

Distribución, hábitat y fenología. Sudeste de Bolivia y Norte de la Argentina, en las provincias de Jujuy, Salta y Tucumán. Habita en las selvas de la provincia fitogeográfica de las Yungas en serranías entre 1000 y 1700 m, generalmente apoyada sobre otros arbustos o árboles. Florece en otoño, invierno y primavera, de febrero a septiembre.

Justicia mandoni es un arbusto apoyante de selva que se caracteriza por las grandes flores rojo-moradas en espigas de aspecto unilateral. Se asemeja a *J. dumetorum*, pero esta última es de porte menos elevado, sus inflorescencias no son unilaterales, y sus flores tienen labios más cortos en relación a la longitud del tubo basal. Por un error involuntario, recientemente se trató a *J. mandoni* como especie endémica de Argentina (Ezcurra, 1999), a pesar de que su distribución abarca el sur de Bolivia. *Justicia tucumanensis* es un nomen nudum con el que originalmente se denominó a esta especie en Argentina (Lillo, 1937).

Material seleccionado. ARGENTINA. **Jujuy:** Capital, Zapla, Mina 9 de Octubre, subida a la antena, *Cabrera 32659* (SI). **Salta:** Caldera, ca. Abra de Los Sauces, *Cabrera 34135* (K, SI); Caldera, Ruta 9, km 1642, 2 km al N de Ojo de Agua, 5 km de Abra de Santa Laura, *Novara 8055* (M, SI); Santa Victoria, Camino de Toldos al Lipeo, ca. 20 km de Toldos, *Legname y Cuezzo 8463* (LIL); Anta, campo Las Heras, *Morello 966* (LIL); Rosario de la Frontera, *Venturi 9338* (K). **Tucumán:** Tafí, quebrada de los Sosa, Arroyo Azucena, *Múlgura 1079* (SI); Chicligasta, Piscicultura, *Meyer 13853* (LIL); Barrayacu, Barrayacu, *Türpe 40* (LIL); Famaillá, Villa Nogués, *Venturi 1799* (SI).

25. Justicia oblonga (Nees) Lindau, in Engler & Prantl, Nat. Pflanzenfam. 4 (3b): 350. 1895. *Rhytiglossa oblonga* Nees, in Martius, Fl. Bras. 9: 124. 1847. TIPO: Brasil. Río Grande do Sul: Porto Alegre, *Sellow s.n.* (sintipo, B destr., fot. F 8847!); Uruguay. Santa Lucía y San Lorenzo, *Sellow s.n.* (sintipo, B destr.); sin loc., *Sellow s.n.* (probable isosintipo, K!).

Hierba perenne, rizomatosa en la base, con tallos erectos, subcilíndricos, de hasta 60 cm long., pubérulos. Hojas opuestas con pecíolo de 0.2–0.4 cm long. y lámina oblongo-elíptica de 2–5 cm long. por 1.2–2 cm lat., acuminada en el ápice, cuneada y algo decurrente en la base, entera, coriácea, pubérula en el haz, pubescente sobre la nervadura en el envés. Inflorescencias formadas por espigas densas, sésiles, terminales o en las axilas de las hojas superiores, a veces formando racimos de espigas en la porción terminal de los tallos, con las hojas reducidas. Brácteas lanceoladas, rígidas, de 5–7 mm long., pubérulas, ciliadas. Cáliz de cerca de 5 mm long., con los 4 segmentos rígidos, lineales, subulados, dorsalmente pubérulos, ciliados. Corola pálido lilacina a violácea de ca. 1 cm long., con tubo de 0.5–0.6 cm long., el labio superior erecto, de 3.5 mm long. por 1 mm lat., el labio inferior ancho, trilobado, de ca. 3 mm long., con estrías blancas en la fauce. Estambres con filamentos de aprox. 2 mm long.; teca apical perfecta, de contorno ovado, de ca. 1 mm long., la otra inserta más abajo en el filamento, más pequeña, angosta y basalmente caudada. Cápsula de contorno obovado, de aprox. 8 mm long. por 3 mm lat., cortamente sólido-estipitada en la base, glabrescente y de paredes finas. Semillas 4, de ca. 1 mm diám., con pelos cortos y gloquidiados; retináculos de ca. 1 mm long., semiobtusos.

Ilustraciones. Ezcurra y Acosta Castellanos, 1997: 109.

Distribución, hábitat y fenología. Sur de Brasil, Uruguay, noreste de Argentina y Paraguay oriental. Habita en ambientes húmedos. Florece principalmente en verano y otoño, de noviembre a abril.

Justicia oblonga se caracteriza por sus flores de aprox. 1 cm long., en espigas densas con brácteas pequeñas. Por las características de sus inflorescencias, anteras y sus cápsulas y semillas indudablemente pertenece a *Justicia* sect. *Chaetothylax* (Nees) V. A. W. Graham (Tabla 1), a pesar de que sus corolas poseen un tubo corto, lo que no es muy

frecuente en esta sección (Ezcurra & Acosta-Castellanos, 1997).

Material seleccionado. ARGENTINA. **Misiones:** Apóstoles, Apóstoles, campos, *Burkart 14443* (SI); Candelaria, Santa Ana, *Rodríguez 288* (SI); San Javier, San Javier, *Krapovickas 15161* (CTES, SI); Leandro Alem, Paso Carreta, *Krapovickas 15021* (CTES, SI); Candelaria, Berón de Astrada, Yabebyry, *Montes 841* (SI); San Ignacio, Ayo. Macaco, *Schwarz 5706* (LIL); Cainguás, ruta 19, Km 252, *Schwindt 3065* (LIL). **Corrientes:** Ituzaingó, 15 km E de Ruta 12, camino a San Carlos, *Krapovickas 17978* (CTES); Santo Tomé, Estancia Garruchos, potrero Puente, *Krapovickas 21611* (CTES); Santo Tomé, Ea. Timbó, Ayo. Ciriaco y Ruta 40, *Schinini 23450* (CTES, LIL). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 5929* (BM, G, K, LIL, SI); Ñacunday, *Montes 9806* (LIL); Ñacunday, *Montes 10933* (LP). **Guaira:** Borja, *Montes 16162* (LIL); Iturbe, *Montes 15762* (LIL); Yegua Porá, *Montes 16383* (LIL).

26. Justicia oranensis De Marco & Ruiz, Publ. Especial Inst. Lillo: 46, fig. 1 y láms. 1 y 2, 1976. TIPO: Argentina. Salta: Oran, camino a la Finca de Jakulica, a 8 km del puente del Rio Bermejo, 600 m s.n.m., *Legname y Cuezzo 8564c* (holotipo, LIL!).

Arbusto ramoso de 1–3 m alt., con ramas subcilíndricas, las jóvenes cuadrisulcadas, con dos bandas longitudinales pilosas a lo largo de los entrenudos. Hojas con pecíolo de 1–4 cm long. y lámina ovada o elíptica de 5–12 cm long. por 3–8 cm lat., aguda y levemente acuminada en el ápice, cuneada en la base, parcialmente decurrente sobre el pecíolo, con las venas principales marcadamente prominentes y notorias en el envés, las secundarias arqueadas y paralelas, la nervadura en general pubescente. Flores sésiles dispuestas en espigas densas y bracteadas que se agrupan en racimos o panojas laxos, pedunculados, más largos que las hojas, en las axilas de las hojas superiores. Brácteas florales obovadas, de 5–8 mm long. por 3–5 mm lat., redondeadas, corta y densamente glanduloso-pubescentes; bractéolas oblongas, de aprox. 6 mm long. por 2 mm lat., obtusas, glandulosas. Cáliz profundamente 5-partido, con los segmentos lanceolados, de 6–7 mm long. por 1–2 mm lat., agudos, levemente glandulosos. Corola rojo-anaranjada, de cerca de 2.5 cm long., con tubo de 1.2 cm long., ensanchado a 3–4 mm diám. en la garganta, y labios de 1 cm long., el posterior bidentado, el anterior trilobado, con los lóbulos de 1 mm long. Estambres con filamentos de 1.5 cm long., y anteras con tecas a distinta altura: la superior separada por el conectivo y oblicua, de 2 mm long., la inferior algo más larga, apendiculada en la base. Cápsula de 1.3–1.5 cm long., estrechada y sólida en la mitad inferior, la porción superior inflada y 4-seminada, glanduloso-pubérula. Semillas suborbiculares de 3 mm diám., tuberculadas. Jaculatores de 2 mm long.

Ilustraciones. De Marco y Ruiz, 1976: 47, 56 y 57. Ezcurra, 1993a: 341.

Distribución, hábitat y fenología. Sur de Bolivia y norte de la Argentina, en las provincias de Jujuy, Salta y Tucumán. Habita en selvas bajas de la provincia fitogeográfica de las Yungas entre 500 y 1600 m, y florece en invierno y primavera, de julio a noviembre. Especie llamativa por sus panojas de flores rojas, según De Marco y Ruiz (1976) es fácilmente cultivable y se puede propagar por estacas.

Justicia oranensis es una especie llamativa por sus panojas de espigas de flores rojo-anaranjadas, y según De Marco y Ruiz (1976) es fácilmente cultivable y se puede propagar por estacas. *Justicia schreiteri* Lillo es un nomen nudum que se utilizó para esta especie (Lillo, 1937).

Material seleccionado. ARGENTINA. **Jujuy:** Ledesma, Caimancito, *Cabrera 27954* (SI); Ledesma, PN Calilegua, *Cabrera 32149* (SI). **Salta:** Santa Victoria, camino de Los Toldos al Lipeo, *Legname y Cuezzo 9707* (LIL); Tabacal, *Martínez Crovetto 3376* (LIL); Gral. José de San Martín, Tartagal, *Schreiter 11372* (SI); Orán, Cedral, *Rodríguez 1045* (LIL); Orán, Vado Hondo, *Legname 7043 C* (LIL). **Tucumán:** sin loc., *Baer 80* (SI).

27. Justicia pectoralis Jacquin, Enum. Syst. Pl. 11. 1760. *Dianthera pectoralis* (Jacq.) Murr., Syst. Veg. Ed. 14, 64. 1784. *Stethoma pectoralis* (Jacq.) Raf., Fl. Tellur. 4: 61. 1838 (1836). *Rhytiglossa pectoralis* (Jacq.) Nees, in Bentham, London J. Bot. 4: 637. 1845. *Ecbolium pectorale* (Jacq.) Kuntze, Revis. Gen. Pl. 2: 487. 1891. *Psacadocalymma pectorale* (Jacq.) Bremek., Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 45: 55. 1948. TIPO: Ilustración en Jacquin, Selec. Stirp. Amer. Hist., t. 3. 1763 (lectotipo, aquí designado ante la ausencia de ejemplar tipo, ver Daniel, 1995).

Hierba pequeña, con tallos ascendentes, radicantes en los nudos inferiores, de hasta 30 cm alt. y 1 mm diám., pubescentes. Hojas con pecíolo de 3–4 mm long., lanceoladas a ovado-lanceoladas, de 4–6 cm long. y 1–2 cm lat., agudas en el ápice, redondeadas en la base, enteras o levemente crenadas, levemente pubescentes sobre las venas. Flores en espigas unilaterales terminales y axilares, simples (en el material de Argentina y Paraguay) o ramificadas, a veces agrupadas en inflorescencias paniculiformes, de 4–10 cm long., con pedúnculos

de 1.5–2.5 cm long. y entrenudos de menos de 1 cm long.; brácteas lanceoladas de 2.5–4 mm long. por 0.5 mm lat., y bractéolas lanceoladas de 2 mm long., ambas pubérulas. Cáliz 4-partido con segmentos de 3.5 mm long. y 0.25 mm lat., obtusos, pubérulos. Corola blanca de 0.8–1.2 cm long. con tubo basal de 5 mm long. por 2.5 mm diám. en la fauce; labio posterior ovado, de 3 mm long. y ca. 2 mm lat., obtuso, y labio inferior de 5 mm long., trilobado, con los lóbulos de 3 mm long. y ca. 2 mm lat., el del medio algo más ancho y con manchas rosadas en la fauce. Estambres exertos, inclusos debajo del labio posterior. Cápsula de ca. 1 cm long., superiormente inflada y 4-seminada. Semillas orbicular-oblongas, aplanadas, de ca. 1 mm diám., pusticuladas, pardo-oscuras.

Ilustraciones. Durkee, 1986: 12.

Distribución, hábitat y fenología. América tropical hasta el Sur de Brasil, y Paraguay oriental y regiones limítrofes de Argentina. En el sur de su distribución habita en el sotobosque de bosques estacionalmente secos, generalmente sobre suelo arenoso. Florece en otoño y primavera, de septiembre a abril.

El material de *Justicia pectoralis* de Paraguay y Argentina se diferencia de la mayoría de los ejemplares de esta especie que habitan más al norte por el porte bajo y las espigas terminales generalmente simples y no agrupadas en inflorescencias paniculiformes. Esta forma empobrecida podría deberse al efecto de una temporada favorable más corta por efecto de su crecimiento a una mayor latitud geográfica, con veranos de menor duración. Esta morfología se asemeja a la descripción de *Justicia sarmentosa* (Nees) Lindau basada en *Rhytiglossa sarmentosa* Nees (Brasil. S. loc., *Sellow 56*, holotipo, B destr.). La ausencia de material tipo asociado a este epíteto hace dudosa su identificación.

Material seleccionado. ARGENTINA. **Formosa:** Matacos, Ing. Juarez, chacra mataca, 3 km camino al R. Bermejo, *Maranta 295* (SI); Ing. Juarez, Toldería Toba, 1 km al N del pueblo, *Arenas 2283* (CORD, SI). PARAGUAY. **Alto Paraguay:** San Carlos del Alto Paraguay, *Molas 1073* (PY). **Boquerón:** Chaco Paraguayo, ruta Trans Chaco, *Schinini y Palacios 25788* (CTES). **Chaco:** Mayor Pedro Lagerenza, selva rivereña del Río Timane, *Schinini y Bordas 14938* (CTES, G). **Nueva Asunción:** Teniente Primero A. Picco, *Spichiger et al. 2298* (G).

28. Justicia phyllocalyx (Lindau) Wasshausen & C. Ezcurra, Candollea 52: 175. 1997. *Poikilacanthus phyllocalyx* Lindau, Engl. Bot. Jahrb. 25, Beibl. 60: 48. 1989. TIPO: Brasil. Goyaz: inter As Brancas et Cocal, *Glaziou 21876* (holotipo, B destr., fot. F 8785!; isotipo, K!).

Sericographis macedoana Rizzini, Arq. Jard. Bot. Rio Janeiro 8: 357, t. 7 y 8, f. 3. 1948. TIPO: Brasil. Minas Gerais: Uberlandia, *Macedo 952* (holotipo, RB fot. US!).

Sericographis macedoana Rizzini var. *elegans* Rizzini forma *redacta* Rizzini, Dusenia 3: 189. 1952. TIPO: Brasil. Minas Gerais: Ituiutaba, *Macedo 1617* (holotipo, RB; isotipo, US!).

Hierba erecta, de 20–70 cm alt. con rizoma en la base, y tallos poco ramificados, cilíndricos, glabros a pubescentes o cortamente tomentosos. Hojas cortamente pecioladas, anchamente elípticas, de 3–6(–8) cm long. y 1.5–3 cm lat., agudas, cuneadas, glabras a densamente pubérulas o cortamente tomentosas. Inflorescencias en espigas terminales o axilares de 3–8 cm long., sésiles a cortamente pedunculadas, alternadamente anisofloras (una sola de cada par de brácteas portando una flor con sus dos bractéolas en la axila); brácteas lineal-lanceoladas, de 10–15 mm, más o menos glanduloso-pubérulas y seríceas; bractéolas lineales, de 8–10 mm long., pubérulas o glabras. Cáliz profundamente 5-partido, con los segmentos subiguales, elíptico-ovados, de 1.2–1.5 cm long. por 3–4 mm lat., agudos o acuminados, pubérulos o glabros, trinervados, con el nervio medio marcado. Corola blanquecina, de ca. 2 cm long., con el tubo de 1.3 cm long., acampanado, hasta de 0.7 cm diám. en la fauce, el lóbulo posterior cóncavo, anchamente ovado, de ca. 1 cm long. y 0.7 cm lat., bidentado, el anterior trilobado, reticulado-venoso en la fauce, con los lóbulos anchamente oblongos, de ca. 1 cm long. y 8 mm lat., redondeados. Estambres exertos por debajo del labio posterior, las tecas marcadamente superpuestas, separadas por un conectivo ancho, la inferior apendiculada en la base. Cápsula desconocida.

Ilustraciones. Figura 11.

Distribución, hábitat y fenología. Sudoeste de Brasil, y noreste de Paraguay en la región del Amambay. Habita en cerrados, en bordes de bosque. Florece en verano y otoño, de enero a abril.

Justicia phyllocalyx se asemeja a otras especies de *Justicia* sect. *Simonisia* como *J. lilloi* y *J. rusbyi*, por lo que se la ubica en esta sección (Tabla 1). Al igual que estas especies, posee polen biporado, pero con ínsulas sobre toda su superficie, no solamente en hileras a los costados de los poros. En esto se asemeja a especies de *Poikilacanthus*. El polen 4- u 8-porado y la exina con ínsulas en toda su superficie que le dan un aspecto facetado es característico de *Poikilacanthus* (Daniel, 1991, 1998), pero el polen de esta especie no coincide totalmente con el de *Poikilacanthus*. A pesar de las ínsulas en toda su superficie, debe ser tratado en

Figura 11. *Justicia phyllocalyx.* —A. Rama con flores. —B. Nudo con bráctea, bractéolas y cáliz. —C. Corola. —D. Corola abierta con androceo. —E. Cápsula abierta sin semillas. *Hassler 8423* (BM, MO), *Ezcurra 1831, 1840* (SI).

Justicia por poseer 2 poros y por la disposición de las ínsulas, y por eso fue transferido a este género (Wasshausen & Ezcurra, 1997).

Material seleccionado. PARAGUAY. **Amambay:** Arroyo Primero, in regione cursus superioris fluminis Apa, *Hassler 8423a* (G); in regione cursus superioris fluminis Apa, *Hassler 8423* (BM, G, K, LIL, NY, P, W); Parque Nacional Cerro Corá, open campo, NE of headquarters, *Solomon 7055* (MO, PY), *7056* (MO); Sierra de Amambay, ad marginem silvarum pr. Estrella, *Rojas 10152* (G, MO).

29. Justicia polygaloides (S. Moore) Lindau, Bull. Herb. Boiss. Ser. 2, 3: 633. 1903. *Dianthera polygaloides* S. Moore, Trans. Linn. Soc. Ser. 2, 4: 433. 1895. TIPO: Brasil. Mato Grosso: Santa Cruz, *Moore 667* (holotipo, K!; isotipo, B destr., fot. F 8855!).

Hierba pequeña, con tallos ascendentes, radicantes en los nudos inferiores, de hasta 30 cm alt. y 1.5 mm diám., glabros o pubérulos. Hojas subsésiles o cortamente pecioladas, lanceoladas o an-

gostamente oblongas, de 3–6 cm long. y 0.4–1 cm lat., agudas en el ápice, cuneadas en la base, enteras, generalmente glabras. Flores en espigas terminales simples, de 3–8 cm long., con pedúnculos de 1.5–4 cm long. y entrenudos de menos de 1 cm long.; brácteas lanceoladas de 1.5–4 mm long. por 0.5 mm lat., y bractéolas triangulares de 2–3 mm long., glabras o pubérulas. Cáliz 4-partido con segmentos de 3–5 mm long. y 0.25 mm lat., acrescente. Corola lilacina de 1 cm long. con tubo basal de 5 mm long. por 2.5 mm diám. en la fauce; labio posterior ovado, de 3 mm long. y ca. 2 mm lat., obtuso, y labio inferior de 3 mm long., trilobado, con los lóbulos de 2 mm long. y ca. 2 mm lat., el del medio algo más ancho y con dibujo pectinado-rugoso, blanco, en la fauce. Estambres exertos, inclusos debajo del labio posterior, con las anteras con las tecas superpuestas de ca. 1 mm long., la inferior oblicua. Cápsula de contorno elíptico, de 0.7 mm long. y 2 mm grosor, glabra. Semillas 4, aplanadas, de ca. 1 mm diám., diminutamente verrucosas.

Ilustraciones. Figura 12.

Distribución, hábitat y fenología. Sudoeste de Brasil y Paraguay oriental. Habita frecuentemente en prados ribereños. Florece en primavera y verano, de septiembre a febrero.

Justicia polygaloides se caracteriza por las hojas lanceoladas o angostamente oblongas y las flores de aprox. 1 cm long. en espigas terminales simples. Es una especie relativamente rara, que ha sido coleccionada pocas veces, en general en prados ribereños. El ejemplar de Argentina, Entre Ríos, presenta una distribución anómala, pero se asemeja al resto del material.

Material seleccionado. ARGENTINA. **Entre Ríos:** Concordia, Balneario La Tortuga Alegre, al N de Concordia, *Bacigalupo 997* (SI). PARAGUAY. **Alto Paraguay:** Puerto Casado, *Rojas 2198* (SI). **Concepción:** Pr. Concepción, *Hassler 7633* (BM, G, NY). **Guairá:** en prados Villa Rica, *Jörgensen 4237* (SI pro parte). **Presidente Hayes:** Gran Chaco, Loma Clavel, *Rojas 2631* (BM, G, K, NY); in regione cursus inferioris fluminis Pilcomayo, *Rojas 669* (G). **San Pedro:** Colonia Primavera, *Woolston 799* (SI).

30. Justicia ramulosa (Morong) C. Ezcurra, Bol. Soc. Argent. Bot. 25: 350. 1988 (Octubre). *Beloperone ramulosa* Morong, Ann. New York Acad. Sci. 7: 194. 1893. *Justicia ramulosa* (Morong) V. A. W. Graham, Kew Bull. 43: 604. 1988 (Noviembre). TIPO: Paraguay. Asunción: *Morong 706* (holotipo, NY!; isotipos, BM!, E!, G!, MO!, NY!, K!, US!).

Beloperone tetramerioides Lindau, Bull. Herb. Boissier 3: 488. 1895. *Justicia tetramerioides* (Lindau) V. A. W. Graham, Kew Bull. 43: 603. 1988. TIPO: Bolivia. Yapacani, 400 m, July 1892, *Kuntze s.n.* (holotipo, B destr., fot. F 8948!; isotipo, NY!).

Beloperone cochabambensis Rusby, Mem. Torrey Bot. Club 6: 103. 1896. *Justicia cochabambensis* (Rusby) V. A. W. Graham, Kew Bull. 43: 603. 1988. TIPO: Bolivia. *Bang 1215* (holotipo, NY!; isotipos, BM!, E!, K!, M!, US!, W!).

Beloperone pseudociliata Mildbr., Notizblatt 9: 1159. 1927. *Justicia pseudociliata* (Mildbr.) V. A. W. Graham, Kew Bull. 43: 603. 1988. TIPO: Bolivia. *Steinbach 7137 bis* (holotipo, B destr., fot. F 8938!; isotipos, BM!, K!, NY!, UC fot. US!).

Hierba sufruticosa con rizoma leñoso en la base y tallos erectos, de 0.40–1 m alt., subcilíndricos, cuadrisulcados, con dos líneas pilosas longitudinales en su juventud. Hojas con pecíolo de 1–3 cm long. y lámina elíptica de 4–11 cm long. por 2–5 cm lat., aguda en el ápice, cuneada en la base y algo decurrente sobre el pecíolo, adpreso-pubérula, con las venas principales prominentes en el envés. Inflorescencias en espigas apicales y en las axilas de las hojas superiores, densas, formadas por flores sésiles con dos bractéolas en las axilas de brácteas decusadas e imbricadas. Brácteas elípticas a angostamente obovadas, de 1–1.5 cm long. por 3–5 mm lat., foliáceas, agudas y mucronadas, pubérulas, ciliadas, con las venas principales muy prominentes en el envés; bractéolas lineales de 6–8 mm long., agudas, ciliadas, con la vena media prominente. Cáliz profundamente 4-partido, con los 4 segmentos lanceolados, de 6–7 mm long., ciliados. Corola de color rojo-vinoso a violácea, de 3 cm long., con el tubo angosto, de 2 cm long. por 2–3 mm diám.; labios de 1 cm long., el superior angosto, de 4 mm lat., levemente bidentado, el inferior trilobado, los lóbulos de 4 mm long. por 3 mm lat. Estambres con filamentos de cerca de 1 cm long., las anteras con tecas superpuestas, la superior de 1.5 mm long., la inferior más pequeña y espolonada en la base. Cápsula de contorno angostamente obovado, de menos de 1 cm long., cortamente estipitada en la base, de paredes finas. Semillas aplanadas, de menos de 2 mm diám., pardas, con pelos cortos y gruesos en toda su superficie; retináculos agudos.

Ilustraciones. Ezcurra, 1993a: 347.

Distribución, hábitat y fenología. Perú, Bolivia, sudeste de Brasil, Paraguay y norte de la Argentina, en bosques húmedos a menos de 500 m de elevación. Florece todo el año, principalmente en otoño, de mayo a junio.

Justicia ramulosa se caracteriza por sus flores rojo-moradas en espigas densas con brácteas imbricadas, elípticas. Es una especie variable que po-

Figura 12. *Justicia polygaloides.* —A. Planta con flores. —B. Flor con bráctea, bractéolas, cáliz, corola, estambres y estilo. —C. Corola abierta con androceo. —D. Cápsula abierta. —E. Semilla. *Woolston 799* (SI), *Jörgensen 4237* (SI).

see una distribución amplia en América del Sur, desde Perú hasta el norte de Argentina. Se asemeja mucho a la especie descripta para Guatemala bajo el nombre de *Chaetothylax cuspidatus* Gibson (Guatemala. *Pittier 1792*; isotipo, US!) y a *Justicia teletheca* T. F. Daniel (Mexico. *Breedlove 56314*; isotipo, K!), y las tres parecen estar muy estrechamente relacionadas.

Material seleccionado. ARGENTINA. **Corrientes:** San Cosme, Paso de la Patria, Costa Toledo, *Meyer 9067* (LIL). **Formosa:** km 139 del FC, *Jörgensen 2336bis* (SI); Guaycuiec, *Jörgensen 2336 pp* (LIL). **Jujuy:** Ledesma, Confluencia del Río Piedras y Arroyo Pantanoso, *Fabris 7302* (LP). **Misiones:** Salto Iguazú, *Lillo 10520* (LIL); Puerto Aguirre, *Rojas 8070* (LIL). **Salta:** Orán, Río Pescado, Pintascayo, *Borsini 613* (LIL); Iruya, *Pierotti 6620* (LIL); San Martín, Grl. Ballivián, El Saladillo, *Legname 10151 C* (LIL). PARAGUAY. **Alto Paraná:** Reserva Itabó, *Caballero Marmori 395* (CTES, MO). **Amambay:** in alta planitie et declivibus Sierra de Amambay, in silvis Punta Pora, *Rojas 10463* (BM, G, K, NY, P, W); Parque Nacional Cerro Corá, *Hahn 2481* (G, MO, US). **Central:** L'Assomption, dans les bois, *Balansa 2448* (BM, G, K, P). **Cordillera:** ad. marg. laqus Ypacaray, *Hassler 3174* (BM,

G, K, LIL, MO, NY, P, W); Cordillera de Altos, *Hassler 2977* (BM, G, K, MO, NY, P, W); Paraguaria centralis, in regione lacus Ypacaray, *Hassler 11701* (BM, K, LIL, MO, NY, SI, US). **Guairá:** Tororo, Propiedad de Raul Alvarenga, *Soria 2670* (MO). **Paraguarí:** Guarapi, dans les bois, *Balansa 3296* (BM, G, P); Macizo Acahay, W side of E peak, *Zardini 5882* (MO, US); Mbatoví, Montain Forest on rocks of cerrado type, *Zardini y Velásquez 13143* (MO); Parque Nacional Ybicuí, 1 km around administration area, *Zardini 4973* (MO, US). **San Pedro:** Colonia Primavera, *Woolston 688* (K, LIL, SI, US). **S. dep.:** s. loc., *Zardini y Velásquez 12954* (MO).

31. Justicia riojana Lindau, Bot. Jahrb. 19(48): 19. 1894. TIPO: Argentina. La Rioja: Sierra de Famatina, Los Berros, *Hieronymus y Niederlein 588* (isosintipo, CORD!); entre La Encrucijada y Las Cuevas, 3 May 1879, *Hieronymus y Niederlein 546* (isosintipo, CORD!); Sierra de Velasco, Cuesta de la Puerta de Piedra, 8–11 Feb. 1879, *Hieronymus y Niederlein 46* (isosintipo, CORD!).

Arbusto ramoso, de 1–1.50 m alt., con ramas erectas, cilíndricas, las jóvenes verdosas y octocostadas, con estrías marcadas entre las costillas, generalmente glabras. Hojas cortamente pecioladas, angostamente lanceoladas a lineares, de 2–4(–6) cm long. por 0.1–0.3 cm lat., agudas, cuneadas en la base, generalmente glabras, pubérulas solamente sobre la vena media en el envés. Flores sésiles o cortamente pediceladas, con dos bractéolas en la base, solitarias en las axilas de las hojas superiores de las ramas principales, o de ramitas laterales, formando en conjunto espigas laxas y foliosas; bractéolas lanceoladas de cerca de 1 cm long. Cáliz acampanado, de ca. 1 cm long., levemente 5-partido, con los lóbulos triangulares, subiguales, de 3 mm long., foliáceos, generalmente glabros. Corola azul violáceo o lilacina de 2–2.5 cm long., pubérula, con tubo corto de cerca de 1 cm long., ensanchado en una garganta de aproximadamente 0.8 cm diám., los labios de 1–1.3 cm long., el anterior trilobado hasta la mitad, con la fauce, convexa y transversalmente rugoso-venosa. Estambres insertos en la base de la garganta, las anteras con las tecas subparalelas, una por encima de la otra, la inferior generalmente apendiculada en la base. Cápsulas obovoides, robustas, glabras, de 1.3–1.8 cm long. por 5–6 mm diám., con la mitad inferior sólida y lateralmente comprimida. Semillas generalmente 4, suborbiculares, lisas, de 4–5.5 mm diám., con un engrosamiento en el borde interno; retináculos obtusos.

Ilustraciones. Ariza-Espinar, 1971.

Distribución, hábitat y fenología. Endémica de la provincia de La Rioja. Su distribución está restringida a las sierras de Famatina y Velasco, entre los 1300–3300 m s.m. Habita en barrancos y en fondos de riachos secos. Florece en verano, de noviembre a febrero.

Nombre vulgar. "Pichanilla" (Ariza, 1971).

Justicia riojana es muy afín a *Justicia tweediana* en las flores axilares solitarias y las semillas lisas con reborde engrosado, pero se diferencia por las hojas muy angostas y los segmentos del cáliz soldados cerca de dos tercios de su longitud. Es considerada forrajera.

Material seleccionado. ARGENTINA. **La Rioja:** Famatina, Los Corrales, *Cabrera 27228* (SI); Famatina, La Batea, Sa. Famatina, *Hunziker, A. 1869* (SI); Felipe Varela, Sierra de Sañogasta, falda W, subiendo desde Aicuña hacia el ESE, *Hunziker, A. 22854, 22863* (CORD); Sa. Famatina, camino a la Mina La Mexicana, *Kiesling 6402* (SI); Chilecito, Cuesta de Miranda, *Cabrera 27112* (SI); Gral. Lavalle, W de Cuesta de Miranda, *Kiesling 6780* (SI).

32. Justicia rusbyi (Lindau) V. A. W. Graham, Kew Bull. 43: 605. 1988. *Chaetochlamys rusbyi* Lindau, Bull. Herb. Boiss. 3: 491. 1895. TIPO: Bolivia. La Paz: Guanai, *Rusby 1117* (isosintipo, BM!, K!, NY!); Santa Cruz, 380 m, June 1892, *Kuntze s.n.* (isosintipo, NY!, US!).

Ruellia lanceolata Morong, Ann. New York Acad. Sci. 7: 193. 1893, non *Justicia lanceolata* (Chapman) Small, 1933. TIPO: Paraguay. Paraguarí: central Paraguay betwen Pirayú and Jaguarón, 8 Abr. 1989, *Morong 667* (holotipo, NY!; isotipo, US!).

Beloperone mattheusii Lindau, Bull. Herb. Boiss. 6, App. 1: 30. 1898. TIPO: Paraguay. Cordillera: in dumeto pr. Cordillera de Altos, *Hassler 1936* (lectotipo, aquí designado, G!; isolectotipos, K!, P!, NY!).

Hierba sufruticosa, de 0.70–1.50 m alt., con tallos erectos, subcilíndricos, cuadrisulcados, engrosados en los nudos, de color verde amarillento, pubérulos, glabrescentes. Hojas con pecíolo de 0.5–3 cm long. y lámina ovada de 5–12 cm long. por 2–6 cm lat., aguda en el ápice y obtusa a redondeada en la base, algo decurrente sobre el pecíolo, verde clara, pubérula, con cistolitos densamente esparcidos en su superficie, las venas principales prominentes en el envés, amarillentas. Flores sésiles, en espigas truncadas reducidas a flores solitarias acompañadas de varias brácteas formando un fascículo, opuestas en las axilas de las hojas superiores, o en espigas laxas con entrenudos largos, terminales y axilares, con brácteas foliosas muy similares a las hojas pero menores; bractéolas lanceoladas, de hasta 15 mm long., pubérulas y cortamente ciliadas, con el nervio medio prominente. Cáliz profundamente 5-partido, con los segmentos

lanceolados, rígidos, de 15–20 mm long. por 2.5–3.5 mm lat., acuminados y densa y cortamente ciliados, con el nervio medio prominente. Corola lilacina de 3–4.5 cm long., con el tubo blanco, de 1.5–2 cm long. por 3–4 mm diám., la garganta dorsalmente gibosa, de 1.5–2 cm long., poco ensanchada, y los labios de cerca de 1.5 cm long., el posterior erecto, de 6 mm lat., muy levemente bilobado, el anterior lila y profundamente trilobado, reticuloado-venoso en la fauce, con los lóbulos patentes, de 1 cm long. por 6–8 mm lat. Estambres con filamentos de ca. 15 mm long., y anteras con las tecas superpuestas y separadas por el conectivo, ambas de 2.5 mm long., basalmente agudas. Estilo glabro con estigma levemente engrosado y bilobado; ovario glabro y disco en forma de copa, ondulado. Cápsulas de cerca de 1.3 cm long. y 5 mm diám. con el tercio inferior sólida y lateralmente comprimido, y la porción superior engrosada, ovoide y 4-seminada, pubérula. Semillas subesféricas, de 3 mm diám., castañas, lisas; retináculos de 3 mm long.

Ilustraciones. Figura 13.

Distribución, hábitat y fenología. Sur de Perú, sudeste de Bolivia, sudoeste de Brasil y este de Paraguay. Habita en el sotobosque y en matorrales de bordes de selva a 200–800 m de elevación, y es frecuente en claros de selvas degradadas. Florece principalmente en verano, de noviembre a abril.

Justicia rusbyi se caracteriza por las flores grandes, lilacinas y blancas con la garganta gibosa, frecuentemente solitarias en las axilas de las hojas. A veces se encuentran ejemplares de esta especie determinados erróneamente como *Ruellia* en los herbarios, e incluso fue descripta por primera vez bajo el nombre de *Ruellia lanceolata* Morong, tal vez por el color lilacino y el tamaño grande de sus flores que se asemejan superficialmente a algunas especies de *Ruellia* de la región. El epíteto *lanceolata* no se puede utilizar para esta especie en *Justicia* por existir un homónimo anterior (Ezcurra, 1993c).

Material seleccionado. PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 5934* (G, US, SI). **Amambay:** cerca del Parque Nacional Cerro Corá, Cerro Tuyá, *Fernández Casas y Molero 6113b* (MO, NY); in campo in regione cursus superioris fluminis Apa, *Hassler 7749* (G); Pedro Juan Caballero, *Schwarz 11762* (LIL). **Caaguazú:** 2 km E de Caaguazú, ruta 2, *Krapovickas 12525* (CTES); Ruta 2, km 98, *Zardini y Aguayo 10622* (MO). **Caazapá:** Tavaí, Propiedad Trosiuk, *Soria 3310* (MO). **Canindeyú:** Colonia Fortuna, *Arenas 716* (CTES, LIL). **Central:** Nemby, *Vavrek 605* (MO, US); Ñemby, Barrio Industrial, *Bordas 3748* (CTES); Villa Elisa, *Pedersen 3132* (K, MO, SI). **Concepción:** Zw. Río Apa and Río Aquidaban, *Fiebrig 4433* (BM, E, G, K, P). **Cordillera:** Cordillera de Altos, *Fiebrig 567* (E, G, K, W); Emboscada, Segunda Compañía, Itá Trompo, *Bordas y Schmeda 4093* (CTES, NY, US); in regione lacus Ypacaray, *Hassler 12458* (BM, E, G, K, MO, NY, US); Paraguaria centralis, in silva pr. San Bernardino, *Hassler 3017* (BM, G); Silve Cordillera de Altos, *Hassler 3740* (BM, K, MO, NY, P, W). **Guairá:** Cerro Mumuy, *Soria 2991* (G, MO); Colonia Independencia, Villarica, *Pedersen 10148* (K, MO). **Paraguarí:** Cerro Ihú, cerca de Paraguarí, *Arbo et al. 2664* (CTES, US); Cerro Palacios, 5 km N of Paraguarí, forest on SW slope, *Zardini y Aguayo 9806* (MO, US); Paraguarí, *Fiebrig 888* (E, G, K); Parque Nacional Ybycu'í, gallery forest along Arroyo Mina, 3 km N of administration area, *Zardini y Aguayo 11981* (MO, US); Yaguarón, Cerro Corá, *Krapovickas 12328* (CTES, US). **Presidente Hayes:** Paraguay expedition Capt. T. J. Page, *Palmer s.n.* (US). **San Pedro:** in regione cursus sup. fluminis Jejui Guazú, *Hassler 5719* (BM, G, K, MO, NY, P); Primavera, Alto Paraguay, *Woolston 451* (K, LIL, NY, SI), *1471* (K). **S. dep.:** Común cerca monte Mhune III, *Jörgensen 4303* (LIL, MO, NY, SI, US).

33. Justicia saltensis T. Ruiz & De Marco, Lilloa 35(2): 13. 1980 ("1979"). TIPO: Argentina. Salta: Gral. San Martín, Piquirenda a Quebrada de Yacuí, 600 m s.m., 3 Feb. 1925, *Schreiter 3509* (holotipo, LIL 48919!).

Hierba sufruticosa en la base, erecta, de 0.4–1 m alt., con ramitas tenues, subcilíndricas, levemente cuadrisulcadas, pilosas, glabrescentes a la madurez. Hojas con pecíolo de 0.5–3 cm long. y lámina ovada, de 3–10 cm long. por 1.5–4.5 cm lat., cuneada a redondeada en la base, aguda y acuminada en el ápice, pubérula en el haz, y esparcidamente pilosa a pubescente en el envés. Inflorescencias axilares, en espigas unilaterales laxas o en racimos de espigas, más largas que las hojas, las flores sésiles en las axilas de brácteas lineales, con dos bractéolas basales, el raquis levemente hirsuto o glanduloso-pubescente. Brácteas lineales, de 3–5 mm, glandulosas y pubescentes, y bractéolas de 2–3 mm long., glanduloso-pubescentes. Cáliz profundamente 4-partido, con los 4 segmentos angostos, lineales, subulados, de 5–7 mm long., glanduloso-pubérulos. Corola rosada a morada, de 1–1.3 cm long., el tubo basal de 4 mm long., ancho, la garganta de 4 mm long. y 3 mm diám., y los labios de 6 mm long., el posterior de 3 mm lat., levemente bidentado, el anterior de 5 mm lat., profundamente trilobado y reticulado-venoso en la fauce, con los lóbulos de cerca de 2 mm long. y lat. Estambres con filamentos de 5 mm long., las tecas a distinta altura, la superior de 1.5 mm long., la inferior oblicua, separada por el conectivo, algo mayor y apendiculada en la base. Cápsula glanduloso-pubérula de 1.5 mm long. por 4 mm diám., con el tercio inferior sólido y lateralmente comprimido, y la porción superior engrosada, cilíndrica y 4-seminada. Semillas comprimidas, de 2.5 mm

Figura 13. *Justicia rusbyi.* —A. Planta con flores. —B. Nudo con bráctea, bractéolas, cáliz y estilo. —C. Corola con androceo. —D. Cápsula abierta. —E. Semilla. *Pedersen* 3132 (SI), *Woolston 451* (SI).

diám., pardo-oscuras, densamente hirsuto-pubescentes; retináculos de 2 mm long., obtusos.

Ilustraciones. Ruiz y De Marco, 1980: 15.

Distribución, hábitat y fenología. Norte de Argentina, sudoeste de Bolivia y oeste de Paraguay. Habita en el estrato herbáceo de bosques de regiones bajas (500–700 m) del Chaco Serrano de Argentina, y de cerros y serranías del Chaco boliviano y paraguayo. Florece en primavera, verano y otoño, de septiembre a mayo.

Justicia saltensis se caracteriza por las flores medianas de aprox. 1 cm long. frecuentemente dispuestas en racimos de espigas secundifloras laxas, con brácteas pequeñas y glanduloso-pubescentes. Debido a sus características morfológicas, en este trabajo la ubico en la sección *Sarotheca* (Nees) Benth. (Tabla 1). Como enunciaron Ruiz y De Marco (1980), presenta afinidad con especies de América del Norte como *Justicia pringlei* B. L. Robinson.

Material seleccionado. ARGENTINA. **Salta:** Yaquiasmé, a 200 m por el camino al pie de la montaña, *Galetto 186* (SI); Metán, RN 9, 27 km de Metán camino a Gral. Güemes, *Morrone 3087* (SI); Anta, 7 km al S de las Víboras, *Vervoorst 4244* (SI), 8448 (LIL); Orán, Piquirenda a Qda. De Yacui, *Schreiter 3515* (LIL). **Santiago del Estero:** Carlos Pellegrini, Cerro del Remate, *Venturi 5866* (SI). **Tucumán:** Burruyacu, El Morado, *Díaz 10191* (LIL); Burruyacu, El Río, *Peirano 10453* (LIL). PARAGUAY. **Chaco:** Cerro León, *Schinini y Bordas 17793* (CTES); Parque Nacional Defensores del Chaco, Cerro León, Misión Tribu Nueva, *Duré y Brunner 428* (CTES, MO, PY).

34. Justicia squarrosa Grisebach, Abh. Ges. Wiss. Goettingen 19: 226. 1874. *Beloperone squarrosa* (Griseb.) Lindau, Bot. Jahrb. 19(48): 21. 1894. TIPO: Argentina. Córdoba: Ascochinga, *Lorentz* (sintipo, GOET fot. US!); Pasaje, *Lorentz y Hieronymus 301* (probables isosintipos, B destr., fot. F 8947!, G no visto fot. F 26579!).

Jacobinia ciliata Nees, in DC., Prodr. 11: 333. 1847, non *Justicia ciliata* Jacq., Hort. Vindob. 2: 47. 1772–3, nec *Justicia ciliata* (Ruiz & Pav.) Pers., Syn. 1: 23. 1805. TIPO: Argentina. Santiago del Estero, *Tweedie 1261* (holotipo, K!).

Hierba sufruticosa ramosa de 15–30 cm alt., con rizoma leñoso en la base y tallos ascendentes, algunos postrados y radicantes en los nudos, subcilíndricos, cuadrisulcados, glabros o con una línea longitudinal pilosa. Hojas cortamente pecioladas, con la lámina angostamente ovada a lanceolada, de 3–7 cm long. por 0.5–2 cm lat., aguda o acuminada, redondeada en la base y algo decurrente sobre el pecíolo, generalmente glabra. Flores sésiles dispuestas en espigas muy cortas y densas, condensadas en el extremo de las ramitas, cada una en la axila de una bráctea y provista de dos bractéolas basales. Brácteas opuestas, lanceoladas, de cerca de 2 cm long. por 2 mm lat., acuminadas, ciliadas, con largas cerdas extendidas (de hasta 1.5 mm long.) sobre los márgenes; bractéolas lineales, de 2 cm long. por 1 mm lat., largamente cerdoso-ciliadas. Cáliz profundamente 5-partido con los segmentos lanceolados, de 1 cm long. por 1 mm lat., acuminados e hirsuto-pilosos hacia el ápice. Corola violácea o lilacina de ca. 2.5 cm long., con tubo algo más largo que los labios y de 2–3 mm diám., el labio posterior erecto, angosto, de 1–1.2 cm long. por 5 mm lat., bidentado, y el anterior profundamente trilobado, rugoso-venoso y manchado de blanco en la fauce, con los lóbulos de cerca de 1 cm long. por 5 mm lat. Estambres con filamentos de 7 mm long. y tecas a distinta altura, la superior de 2 mm long., la inferior algo más larga, separada por el conectivo y aguda en la base. Cápsula de 1.5 cm long. por 3–4 mm diám., con la mitad inferior sólida y lateralmente estrechada y la superior ovoide. Semillas 4, subglobosas, de 2.5 mm diám., castañas, lisas y lustrosas; retináculos obtusos, de 2 mm long.

Ilustraciones. Ariza-Espinar, 1971: 90. Ezcurra, 1993a: 354.

Distribución, hábitat y fenología. Especie ampliamente distribuida en el sudeste de Bolivia, oeste de Paraguay, y norte y centro de la Argentina, característica de la provincia fitogeográfica Chaqueña occidental. Habita en lugares secos y degradados entre vegetación de monte entre los 500 y 1000 m s.m. Florece en verano y otoño, de enero a junio.

Justicia squarrosa se caracteriza por sus flores lilacinas grandes con el tubo angosto dispuestas en espigas capituliformes densas con brácteas angostas y ciliadas. En estos caracteres parece muy afín a una especie de América Central, *Justicia isthmensis* T. F. Daniel (= *Justicia panamensis* (Lindau) V. A. W. Graham, Panamá. Chagres Valley, *Pittier s.n.*; isosintipo, BM!), y las relaciones entre ambas deberían estudiarse. Es apetecida por el ganado.

Material seleccionado. ARGENTINA. **Catamarca:** La Paz, El Moreno, *Brizuela 927* (LIL); Capayán, Capayán, *Muller 172* (LIL); Valle Viejo, Cuesta del Portezuelo, *Hunziker, A. 15313* (CORD); El Juncal, *Soriano 845* (SI). **Chaco:** Napalpí, Campo Largo, *Buratovich 635* (LIL). **Córdoba:** Colón, Ascochinga, *Giardelli 1173* (SI); Pocho, Sierra de Pocho, falda W al noroeste de Chancaní, *Hunziker, A. 9810* (CORD); Ischilin, Sierra de Copacabana, *Hunziker, A. 14792* (CORD); Tulumba, ca. de L. V. Man-

silla, en las inmediaciones del desvío a Turcal, *Hunziker, A. 25229* (CORD); Capital, C°. de las Rosas, *Pierotti 5131* (LIL). **Jujuy:** San Pedro, San Pedro, *Ahumada 4481* (SI); Santa Bárbara, Pto. Nuevo, *Cabrera 26314* (SI). **La Rioja:** Capital, La Rioja, *Burkart 12528* (SI); San Martín, entre ruta 20 y Ulapes, ca. 16 Km de Ulapes, *Hunziker, A. y Caro 13618* (CORD); Chamical, Qda. De Soria, 8 Km al SE de Chamical, *Hunziker, A. 16647* (CORD). **Salta:** La Viña, 5 km al S de Cnel. Moldes, *Kiesling 5838* (SI); Rosario de la Frontera, 2.3 Km de la ruta 34, camino a San Lorenzo, *Krapovickas y Cristóbal 46675* (LIL); Metán, Lumbrera, *Meyer 16492* (LIL); Anta, Joaquín V. González, *Morello s.n.* (LIL). **Santiago del Estero:** Guasayán, falda oriental de la Sa. de Guasayán, de Santa Catalina a Lavalle, *Botta 138* (SI); Dpto. Ojo de Agua, Cachi, *Di Lullo 27* (SI); Choya, El Salvador, clausura 2, *Legname s.n.* (LIL); Copo, Los Tigres, 3 Km al N de Monte Quemado, *Reic 605* (LIL); C. Pellegrini, Cerro del Remate, *Venturi 5868* (LIL). **San Luis:** Junín, Santa Rosa, Qda. De La Higuerita, *Burkart 13958* (SI). **Tucumán:** Trancas, Berón de Astrada, Tapia, *Diers 46* (SI); Dpto. Trancas, Vipos, *Venturi 2686* (LIL). PARAGUAY. **Boquerón:** Campo Loro, límite con Alto Paraguay, *Schmeda 866* (CTES, US); Estación Experimental Filadelfia, *Vanni 2577* (CTES); Picada entre Teniente Ochoa y Mariscal Estigarribia, a 10 km de Mariscal Estigarribia en claros del bosque, *Soria 1308* (CTES, MO). **Nueva Asunción:** ca. Estancia Copagro, 586 km de Asunción, *Bernardi 20202* (G, US); Estancia La Madelón, piste Trans Chaco pk 635, *Billiet y Jadin 3123* (G); Fortín Teniente Enciso, ruta Trans-Chaco, *Schinini y Bordas 16471* (CTES, G, US); General Eugenio A. Garay, línea de Hito, frontera con Bolivia, *Charpin y Ramella 21485* (G); Ruta Trans-Chaco, *Schinini y Bordas 16375* (CTES).

35. Justicia tocantina (Nees) V. A. W. Graham, Kew Bull. 43: 604. 1988. *Chaetothylax tocantinus* Nees, in Martius, Fl. Bras. 9: 153. 1847. TIPO: Brasil. Goyaz, *Pohl s.n.* (sintipo, W!; isosintipo, M!); Minas Gerais, *Claussen s.n.* (sintipo, P no visto; isosintipo, K!).

Hierba perenne, rizomatosa y leñosa en la base, con tallos erectos subcilíndricos, a veces decumbentes y geniculados, de hasta 50 cm long., pubérulos o glabros. Hojas opuestas con pecíolo de 5–20 mm long. y lámina ovada de 4–10 cm long. por 2.5–5.5 cm lat., acuminada en el ápice, cuneada y algo decurrente en la base, entera, generalmente glabra, con la nervadura prominente en el envés. Inflorescencias formadas por flores sésiles con dos bractéolas en su base, dispuestas en espigas densas enriquecidas por flores derivadas de yemas axilares supernumerarias. Espigas terminales o en las axilas de las hojas superiores. Brácteas y bractéolas lanceoladas, rígidas, de 4–6 mm long., cilioladas, con el nervio medio prominente en el dorso. Cáliz de 5–8 mm long., con los 4 segmentos rígidos, lineales, subulados, con pelos glandulares. Corola rosado–violácea de 2.7–2.9 cm long., externamente pubescente, con tubo angosto de 2 cm long., ampliado en una garganta de ca. 4 mm diam., el labio superior erecto, de 7 mm long. por 2 mm lat., el labio inferior ancho, trilobado, de ca. de 8 mm long., con estrías blancas en la fauce. Estambres con filamentos de aprox. 8 mm long.; teca apical perfecta, de contorno ovado, de 1.5 mm long., la otra inserta más abajo en el filamento, semiestéril, más angosta y basalmente caudada. Cápsula de contorno obovado, de aprox. 7 mm long. por 2.5 mm lat., cortamente sólido-estipitada en la base, generalmente glabra y de paredes finas. Semillas 4, aplanadas, de 1 mm diám., con pelos cortos y gloquidiados; retináculos de 1 mm long., obtusos.

Ilustraciones. Nees, 1847a: 26 (sub *Chaetothylax tocantinus*).

Distribución, hábitat y fenología. Este de Bolivia, sudoeste y centro de Brasil, y extremo norte de Paraguay. Habita en bosques estacionalmente secos. Florece en otoño y primavera, principalmente en abril y mayo.

Justicia tocantina es afín a *Justicia goudotii*, pero se caracteriza por sus flores rosado-violáceas grandes de aprox. 3 cm long. con tubo angosto levemente ampliado en la garganta, dispuestas en inflorescencias espiciformes densas similares a las de *Justicia goudotii*. Es la primera vez que se cita esta especie para Paraguay y Bolivia.

Material seleccionado. PARAGUAY. **Chaco:** Cerro León (Lagerenza), oeste del Cerro, Ramella, *Fortunato y Palese 2970* (G); Cerro León, desde lomada al S (campamento) hasta Meseta Central, *Charpin y Ramella 21733 p.p.* (G); Parque Nacional Defensores del Chaco, Cerro León, *Hahn 1530* (G, MO, PY). BOLIVIA. **Santa Cruz:** Caballero, 8–9 km east of Saipina on road to Pulgina, *Wood 10919* (K); Caballero, ca. 2 km above Comarapa by Rio Comarapa, *Wood 10923* (K).

36. Justicia tweediana (Nees) Grisebach, Abh. Ges. Wiss. Goettingen 19: 225. 1874. *Adhatoda tweediana* Nees, in DC., Prodr. 11: 395. 1847. *Justicia tweediana* (Nees) Benth., in Bentham & Hooker, Gen. Pl. 2(2): 1109. 1876. *Ecbolium tweedianum* (Nees) O. Kuntze, Rev. Gen. Pl. 1(2): 981. 1891. *Poikilacanthus tweedianus* (Nees) Lindau, Bot. Jahrb. 18: 57. 1893. TIPO: Argentina. Córdoba: Río Segundo, *Tweedie s.n.* (sintipo, K!); Parana ("Parama"), *Tweedie s.n.* (sintipo, K!); Buenos Aires, *Tweedie s.n.* (sintipo, K!; isosintipo, BM!); San Luis: Aguadita, *Gillies s.n.* (sintipo, K!; isosintipos, BM!, E!).

Adhatoda tweediana Nees var. *angustifolia* Nees, in DC., Prodr. 11: 395. 1847. Argentina. Parana ("Panama"): *Tweedie s.n.* (sintipo, K); Buenos Aires, *Tweedie s.n.*

(sintipo, K!), *Gillies s.n.* (sintipo, K!); San Luis, *Gillies s.n.* (sintipo, K!).

Justicia campestris Griseb., Abh. Ges. Wiss. Goettingen 19: 225. 1874, non *Rhytiglossa campestris* Nees, in Martius, Fl. Bras. 9: 118. 1847. *Justicia lorentziana* Lindau, Bot. Jahrb. 19(48): 20. 1894. *Ecbolium lorentzianum* (Lindau) O. Kuntze, Rev. Gen. Pl. 3(2): 248. 1898. TIPO: Argentina. Córdoba: Las Peñas, *Lorentz 118* (holotipo, GOET no visto; isotipo, CORD!, fragmento LIL!)

Justicia diamantina Lindau, Bull. Herb. Boiss. 5 (ser. 2): 371. 1905. TIPO: Argentina. Entre Ríos: Diamante, Mar. 1903, *Malme s.n.* (sintipo, B destr.; isosintipos no vistos).

Sufrútice o arbusto ramoso, de 0.50–1.50 m alt., con ramas erectas, cilíndricas, las jóvenes verdosas y octocostadas, con estrías marcadas entre las costillas, generalmente glabras. Hojas cortamente pecioladas, angostamente ovadas a lanceoladas, de 2–4(–6) cm long. por 0.5–1.5(–2.5) cm lat., agudas, cuneadas en la base, generalmente glabras, pubérulas solamente sobre la vena media en el envés. Flores sésiles o cortamente pediceladas, con dos bractéolas en la base, solitarias en las axilas de las hojas superiores de las ramas principales, o de ramitas laterales, formando en conjunto espigas laxas y foliosas; bractéolas lanceoladas de cerca de 1 cm long. Cáliz profundamente 5-partido, con los lóbulos angostamente ovados a lanceolados, subiguales, de 5–8 mm long., foliáceos, generalmente glabros. Corola azul violáceo, lilacina a blanca de 2–2.5 cm long., pubérula, con tubo corto de cerca de 1 cm long., ensanchado en una garganta de aproximadamente 0.8 cm diám., los labios de 1–1.3 cm long., el anterior trilobado hasta la mitad, con la fauce blanca, convexa y transversalmente rugoso-venosa. Estambres insertos en la base de la garganta, las anteras con las tecas subparalelas, una por encima de la otra, la inferior generalmente apendiculada en la base. Cápsulas obovoides, robustas, glabras, de 1.3–1.8 cm long. por 5–6 mm diám., con la mitad inferior sólida y lateralmente comprimida. Semillas generalmente 4, suborbiculares, lisas; retináculos obtusos.

Ilustraciones. Ariza-Espinar, 1971: 96 (sub *Justicia campestris*). Dawson, 1979: 573 (sub *Justicia campestris*). Ezcurra, 1993a: 348.

Distribución, hábitat y fenología. Norte, centro y E de la Argentina, desde Jujuy hasta San Luis, Córdoba, Santa Fé, Entre Ríos y N de Buenos Aires. Vegeta en regiones áridas y semiáridas entre el nivel del mar y 2500 m (según la latitud). Es apetecida como forraje por cabras y ovejas en lugares con escasez de gramíneas. Florece principalmente en verano, de septiembre a mayo.

Nombres vulgares. "Boca de conejo," "palomillo," "alfilla," "alfalfita," "quiebrarao," "escoba dura" (Burkart, 1943, sub *Justicia campestris*).

Justicia tweediana se caracteriza por las flores medianas, solitarias, axilares, de color celeste-lilacino a blanco, y las semillas aplanadas, lisas, con engrosamiento perisférico. Tiene un alto valor como forrajera (Burkart, 1943).

Material seleccionado. ARGENTINA. **Buenos Aires:** San Nicolás, San Nicolás, barrancas, *Cabrera 7192* (SI); Baradero, Baradero, barrancas, *Burkart 8498* (K, SI). **Catamarca:** Andalgalá, Andalgalá, *Jörgensen 982* (SI); Capayán, camino al dique nivelador Capayán, *Legname 7264* (LIL); Santa María, El Sarcito, *Reales 1055* (LIL); Belén, Pozo de Piedras, *Sleumer y Vervoorst 2425* (LIL). **Chaco:** CH, Pampa del Infierno, *Meyer 8570* (LIL); Campo del Cielo, Itín, *Schulz 1095* (LIL). **Córdoba:** Capilla del Monte, *Castellanos s.n.* (LIL); Punilla, Sierra Chica, al N del C° Unpico, *Hunziker, A. 8947* (CORD); San Justo, entre Concepción del Tío y El Tío, *Hunziker, A. 10068* (CORD); Totoral, alrededores del agua en el arroyo Macha, 5 Km al W de Las Peñas, *Hunziker, A. 21843* (CORD); Río Cuarto, entre Berrotarán y Santa Isabel, *Ragonese y Piccinini 9408* (SI); Tercero Arriba, Río Tercero, *Burkart 13368* (SI). **Entre Ríos:** Paraná, Barrancas de Paraná, *Burkart 20647* (SI); Victoria, Victoria, *Meyer 10198* (LIL); Capital, Paraná, barrancas del río, *Solbrig 51* (LIL). **Jujuy:** Tilcara, Huacalera, *Cabrera 11995, 12072, 15515* (LP); Tumbaya, Laguna de Volcán, *Kiesling 4345, 5823* (SI). **La Rioja:** Chilecito, cuesta de Miranda, ruta 40, Km 546, *Hunziker, A. 22674* (CORD); Cuesta de la Cébila, *Kiesling 6410* (SI). **Salta:** Camino a Cachi, pasando Escoipe, *Legname 9005* (LIL); Candelaria, Unquillo, *Schreiter 9358* (LIL); Rosario de Lerma, Campo Quijano, *Venturi 5060* (SI). **San Juan:** San Juan, *Echegaray s.n.* (LIL). **Santa Fé:** Rosario, Rosario, *Pire 3813* (SI). **San Luis:** Capital, alrededores de San Luis, *Covas 1102* (LIL); Pedernera, Villa Mercedes, 4 Km al oeste de la usina, *Anderson 1811* (CORD); Dpto. Pringles, RP 9, cerca de El Volcán, *Kiesling 4718* (SI); Chacabuco, Concarán, 605 m, *Varela 495* (LIL). **Santiago del Estero:** Los Pirpintos, ruta 16, *Legname 7521* (LIL); Copo, Pampa de los Guanacos, *Malvárez 675* (LIL). **Tucumán:** Tafí, entre El Infiernillo y Amaicha del Valle, *Legname y Cuezzo 5514* (LIL); Tafí, Sa. Del Cajón, *Venturi 4438* (SI).

37. Justicia xylosteoides Grisebach, Abh. Ges. Wiss. Goettingen 19: 225. 1874. *Ecbolium xylosteoides* (Griseb.) O. Kuntze, Rev. Gen. Pl. 3(2): 248. 1898. TIPO: Argentina. Santiago del Estero: "antes que se pasa el Saladillo", 4/5 Dic. 1871, *Lorentz 12* (holotipo, GOET no visto; isotipo CORD!).

Beloperone scorpioides Nees, in DC., Prodr. 11: 422. 1847. *Justicia scorpioides* (Nees) Griseb., Abh. Ges. Wiss. Goettingen 24: 262. 1879, non *Justicia scorpioides* L., Sp. Pl. ed. 2: 21. 1762–63. TIPO: Argentina. "Tucumán", Saladillo, *Tweedie 1159* (holotipo, K!, fot. US!).

Arbusto de 1–2 m alt., robusto, ramoso, con ramas erectas, 4-sulcadas en su juventud, general-

mente glabras; ramitas laterales con entrenudos cortos en la base, alargados superiormente. Hojas subsésiles o muy cortamente pecioladas, con lámina angostamente elíptica, ovada, obovada u oblonga de 2–4(–6) cm long. por 0.7–1.5 cm lat., glabra o muy levemente pubérula, glanduloso punteada, obtusa a redondeada en el ápice, cuneada en la base. Espigas sésiles, densas, terminales o axilares, a veces agrupadas en racimos, con brácteas lanceoladas a ovadas, opuestas y decusadas, a veces alternas por desplazamiento y concaulescencia, siempre una fértil y la otra estéril de cada par, las fértiles mayores, de hasta 8(–10) mm long. por 2–4 mm lat., las estériles menores, de 2 mm long. y 1 mm lat., el raquis arqueado; bractéolas triangulares, de 2–3 mm long. y 1 mm lat., escabroso-pubérulas. Cáliz de 3–4 mm long., con los 5 segmentos ovados, agudos, pubérulos. Corola roja, de 3–4.5 cm long., con tubo de 2–2.5 cm long., subcilíndrico, poco ensanchado en la fauce, y labios de 1–1.5 cm long., el posterior apenas bidentado, el anterior profundamente trilobado. Estambres con filamentos de 1.3–1.7 cm long., y anteras con las tecas a distinta altura, la inferior oblicua y apendiculada en la base. Cápsula de 1.3 cm long. por 0.5 cm diám., sólida y lateralmente estrechada en la base, superiormente inflada y 4-seminada. Semillas suborbiculares, aplanadas, de 3–4 mm diám., tuberculado-rugosas, más o menos oscuras.

Ilustraciones. Ariza-Espinar, 1971: 81.

Distribución, hábitat y fenología. Regiones áridas del sur de Bolivia, noroeste de Paraguay y noroeste de Argentina. Habita en claros de montes xerófilos bajos y en matorrales áridos entre 700 y 2300 m s.m. Florece principalmente en verano, de septiembre a mayo.

Tal como lo señaló Lindau (1894), *Justicia xylosteoides* es una especie de afinidades poco claras, tal vez por sus modificaciones en adaptación a la aridez. Esto la hace difícil de ubicar en el sistema de Graham (1988). Por sus espigas simples con brácteas generalmente ovadas, flores grandes y semillas tuberculadas se ubica provisoriamente en la sección *Orthotactus* (Tabla 1). Es una especie llamativa por sus grandes flores rojas, ornitófilas, que merecería cultivarse en climas áridos. Es apetecida por el ganado.

Material seleccionado. ARGENTINA. **Catamarca:** La Paz, Ramblones, *Brizuela 456* (LIL); Fray M. Esquiú, Polcos, ruta 62, *Hunziker, A. 22457* (CORD); Capital, Catamarca, *Nicora s.n.* (SI 18623); Santa María, El Sarcito, *Reales 1043* (LIL); Pachín, entre Catamarca y Cuesta del Totoral, *Villa Carenzo y Legname 1133* (LIL). **Córdoba:** Tulumba, Dean Funes, *Balegno 1191* (LIL); Pocho, entre Bañado de Paja y El Chocolate, en el camino de Villa Dolores a Chancaní, *Hunziker, A. 14694* (CORD); Sobremonte, 6/7 Km al oeste de la plaza de San Francisco del Chañar, rumbo a L. V. Mansilla, *Hunziker, A. y Subils 24951* (CORD); Cruz del Eje, Camino a Soto, *Nicora s.n.* (*SI 17632*). **La Rioja:** Chamical, RP4, 5 Km al N de la Salina La Antigua, *Biurrun 584* (CORD); Capital, Dique Los Sauces, falda de la Sierra de Velasco, *Hunziker, A. 4708* (LIL); Gral. Belgrano, Sierra de Los Llanos, entre Olta y El Dique, *Hunziker, A. 13915* (CORD); Gral. Lavalle, Cuesta de Miranda, *Kiesling 6783* (SI). **Salta:** La Viña, 5 km al S de Coronel Moldes, *Kiesling 5844* (SI); Candelaria, Lomas altas del Cerro Santa Victoria, *Legname 3387* (LIL); Cachi, Bajada de Tin Tin, *Cabrera 30759* (SI); Cafayate, camino de Santa María a Cafayate, a 2 Km de Cafayate, *Legname 8893* (LIL); Metán, entre Gas del Estado y Río Juramento, *Meyer s.n.* (LIL); Molinos, Seclantás a Brealito, *Meyer 12195* (LIL). **Santiago del Estero:** Guasayán, Sa. de Guasayán, *Kiesling 1262* (SI); Pellegrini, Sol de Mayo a Los Baños, *Peirano 9021* (LIL); Río Hondo, Las Termas, *Meyer 12789* (LIL); Choya, desde Puerta Chiquita, yendo hacia Alto Bello, *Subils 3666* (CORD). **Tucumán:** Tafí, Amaicha del Valle, *Burkart 5328* (SI); Trancas, Tapia, *Rodriguez 597* (SI). PARAGUAY. **Boquerón:** Colonia Menno, Estancia Fehr, 68 km NE de Filadelfia, *Krapovickas y Cristobal 44290* (CTES); Picada Sirascuas, *Mereles y Degen 5490* (FCQ). **Nueva Asunción:** 8 km al Norte de Pozo Olga, *Spichiger et al. 2268* (US); Estancia La Madelon, ruta Transchaco, pk 635, bosque seco de quebracho y chorisia, pastoreado, *Billiet y Jadin 3126* (G, MO); Parque Nacional Teniente Enciso, 1 km N of the administration por la picada Bolivia, *Vavrek 334* (MO, US).

38. Justicia yhuensis Lindau, Bull. Herb. Boiss. Ser. 2, 4: 411. 1907. TIPO: Paraguay. In regione fluminis Yhú, Oct. 1905, *Hassler 9568* (holotipo, G!; isotipos, BM!, K!, NY!, P!).

Justicia hylobates Leonard, Sellowia 9: 83, fig. 2. 1958. TIPO: Brasil. Santa Catarina: Itapiranga, Popi, pelo caminho a Sant'Antonio, mata, 200–350 m, 24 Feb. 1957, *Smith, Klein y Schnorrenberger 11727* (holotipo, US!; isotipo, NY!).

Hierba débil enraizadora en la base, de hasta 60 cm alt., con tallos erectos, subtetrágonos, ramificados, longitudinalmente surcados, pubérulos a glabros. Hojas cortamente pecioladas o subsésiles, con la lámina angostamente ovada, de 4–7 cm long. por 1.2–2.5 cm lat., largamente aguda en el ápice, redondeada a levemente cordada en la base, algo discolor, glabra o muy laxamente pilosa. Inflorescencias en espigas terminales y laterales de hasta 12 cm long., laxas, delicadas, con pedúnculos de 2 cm long.; brácteas angostamente triangulares, de 2–3 mm long. y 0.5 mm lat., agudas, aquilladas, glabras o pubérulas; bractéolas de la misma longitud. Cáliz profundamente 4-partido, con los segmentos lanceolados, de 3 mm long. por 0.5 mm lat., agudos, glabros. Corola blanca de ca. 9 mm long. con tubo obcónico de 3–4 mm long. y labios de 4–5 mm long., el posterior triangular, de 2 mm lat. en

la base, obtuso; el anterior trilobado, con los lóbulos de 1.5–2 mm long. y 2.5 mm lat. (los laterales algo menores), redondeados. Estambres exertos hasta la mitad del labio posterior, con las tecas superpuestas, de ca. 1 mm long., separadas por un conectivo ancho, la superior mayor y oblicua, ambas agudas en la base. Cápsula delicada, angostamente claviforme, de 7–8 mm long. por 2 mm diám., sólida y lateralmente estrechada en el tercio inferior, glabra. Semillas aplandas, de 1 mm diám., con papilas cortas; retináculos de menos de 1 mm long.

Ilustraciones. Wasshausen y Smith, 1969: 96 (fig. 14F, G).

Distribución, hábitat y fenología. Sur de Brasil, noreste de Argentina y Paraguay oriental. Habita en bordes de selvas de regiones bajas y florece en primavera y verano, de octubre a mayo.

Justicia yhuensis se caracteriza por sus hojas lanceoladas y sus espigas simples de flores medianas a pequeñas. El nombre *Justicia hylobates* se considera sinónimo de esta especie.

Material seleccionado. ARGENTINA. **Misiones:** Orilla Arroyo Yabotí, *Deginani 1135* (SI); Guaraní, RP 2, Reserva ecológica provincial, 23 km de El Soberbio camino al Parque Prov. Moconá, *Morrone 695* (SI); San Javier, Londero, *Schwarz 4310* (LIL). PARAGUAY. **Amambay:** Sierra de Amambay, ad marginem silvarum ad fl. Aquidaban, *Rojas 9718* (G); Zw. Río Apa und Río Aquidabán, Caballero Cué, *Fiebrig 4813* (BM, E, G, K). **Cordillera:** inter rupas in dumetis Cordillera de Altos, *Hassler 2135* (G). **Concepción:** Río Aquidabán, Paso Horqueta, *Palacios 1873* (MO).

Especies Dudosas o Excluidas

Justicia flexuosa (Nees) Wasshausen & L. B. Smith (citada por Wasshausen & Smith, 1969, para Santa Catarina, Brasil).

Justicia umbrosa (Nees) Lindau (citada por Wasshausen & Smith, 1969, para Santa Catarina, Brasil).

Estos dos nombres son sinónimos de **Poikilacanthus glandulosus** (Nees) Ariza (Ariza-Espinar, 1983; Ezcurra, 1999). *Poikilacanthus* Lindau es un género superficialmente muy similar a *Justicia*, con polen con características algo diferentes (Daniel, 1991, 1998), pero muy relacionado con algunas especies de *Justicia* del Nuevo Mundo a nivel molecular (Mc Dade et al., 2000), por lo que eventualmente podría ser tratado dentro de *Justicia* s. lat. Pero hasta tanto se estudien las relaciones morfológicas y moleculares de un número mayor de especies de *Justicia* del Nuevo Mundo prefiero mantener a *Poikilacanthus* como género separado de *Justicia*. A continuación se da la sinonimia completa de esta especie.

Poikilacanthus glandulosus (Nees) Ariza, Kurtziana 17: 157–161. 1984. *Orthotactus glandulosus* Nees, in Martius, Fl. Bras. 9: 132. 1847. *Adhatoda* umbrosa Nees, in DC., Prodr. 11: 406. 1847, non *Adhatoda glandulosa* Nees, 1847. *Ecbolium umbrosum* (Nees) O. Kuntze, Rev. Gen. Pl. 1(2): 981. 1891. *Justicia umbrosa* (Nees) Lindau, Bot. Jahrb. Syst. 19(48): 20. 1894, non Benth. 1841. TIPO: Brasil. *Sellow 164* (sintipo, B destr., fot. F 8877!).

Justicia spathulata Nees & Mart., Nov. Act. Nat. Cur. 11: 55. 1823, non *Justicia spathulata* Thunb., Fl. Jap.: 22. 1784. *Beloperone spathulata* (Nees & Mart.) Nees, in Martius, Fl. Bras. 9: 136. 1847. TIPO: Brasil. *Sellow s.n.* (holotipo, B destr.; isotipo, K!).

Adhatoda flexuosa Nees, in Martius, Fl. Bras. 9: 148. 1847. *Ecbolium flexuosum* (Nees) O. Kuntze, Rev. Gen. 2: 980. 1891. *Poikilacanthus flexuosus* (Nees) Lindau, Bot. Jahrb. 18: 57. 1893. *Justicia flexuosa* (Nees) Wasshausen & Smith, in R. Reitz, Fl. Ilustr. Catarinense ACAN: 113. 1969. TIPO: Brasil. Río Grande do Sul: entre Porto Alegre y Montevideo, "ad ripas fl. Uruguay", *Sellow 997* (sintipo, B destr., fot. F 8779!; isosintipo, K!); Minas Gerais, Villa Rica, *Sellow s.n.* (sintipo, B destr.), *Martius s.n.* (sintipo, M!); São Paulo, inter Taubaté et Mogy, *Riedel s.n.* (sintipo, LE no visto; isosintipo, NY!); São Paulo, ad oppidulum S. Carlos, *Riedel s.n.* (sintipo, LE no visto).

Ilustraciones. Wasshausen y Smith, 1969: 110 (sub *Justicia flexuosa*, fig. 15 F).

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Apéndice 1

Lista de especies

1. *Justicia aequilabris* (Nees) Lindau
2. *Justicia axillaris* (Nees) Lindau
3. *Justicia baenitzii* (H. Winkler) C. Ezcurra
4. *Justicia brasiliana* Roth
5. *Justicia carnea* Lindl.
6. *Justicia chacoënsis* Wasshausen & C. Ezcurra
7. *Justicia comata* (L.) Lamarck
8. *Justicia corumbensis* (Lindau) Wasshausen & C. Ezcurra
9. *Justicia cuspidulata* (Nees) Wasshausen
10. *Justicia dumetorum* Morong
11. *Justicia floribunda* (C. Koch) Wasshausen
12. *Justicia gilliesii* (Nees) Bentham
13. *Justicia glaziovii* Lindau
14. *Justicia glutinosa* (Bremekamp) V. A. W. Graham
15. *Justicia goudotii* V. A. W. Graham
16. *Justicia hassleri* (Lindau) V. A. W. Graham
17. *Justicia hunzikeri* Ariza Espinar
18. *Justicia jujuyensis* C. Ezcurra
19. *Justicia kuntzei* Lindau
20. *Justicia laevilinguis* (Nees) Lindau
21. *Justicia lilloana* Ariza Espinar
22. *Justicia lilloi* (J. L. Lotti) C. Ezcurra
23. *Justicia lythroides* (Nees) V. A. W. Graham
24. *Justicia mandoni* (Lindau) Wasshausen & C. Ezcurra
25. *Justicia oblonga* (Nees) Lindau
26. *Justicia oranensis* De Marco & Ruiz
27. *Justicia pectoralis* Jacquin
28. *Justicia phyllocalyx* (Lindau) Wasshausen & C. Ezcurra
29. *Justicia polygaloides* (S. Moore) Lindau
30. *Justicia ramulosa* (Morong) C. Ezcurra
31. *Justicia riojana* Lindau
32. *Justicia rusbyi* (Lindau) V. A. W. Graham
33. *Justicia saltensis* T. Ruiz & De Marco
34. *Justicia squarrosa* Grisebach
35. *Justicia tocantina* (Nees) V. A. W. Graham
36. *Justicia tweediana* (Nees) Grisebach
37. *Justicia xylosteoides* Grisebach
38. *Justicia yhuensis* Lindau

Apéndice 2

Índice de exsiccatas

Lista de ejemplares examinados con datos de coleccionista (en orden alfabético) y número de colección. El número entre paréntesis corresponde a la especie a la que pertenece cada ejemplar según la numeración en la lista de especies. Los ejemplares tipo se indican con asterisco (*).

Abbiatti y Claps 221 (18). Aguilar 566 (4). Ahumada 4481 (34); 8234 (3). Anderson 1811 (36); 1936 (17); 4044 (12). Arbo y Tur 2214 (20). Arbo et al. 906 (2); 1652 (10); 1657 (20); 2664 (32). Archer y Rojas 4847 (20). Arenas 143 (10); 287 (9); 716 (32); 1097 (10); 1189 (4); 1457 (10); 2283 (27). Arnott s.n.* (20).

Bacigalupo 997 (29); 1376 (20). Bacle s.n.* (20). Baer 80 (26). Balansa 2448 (30); 2449 (20); 2451, 2451a (20); 2456 (16); 2459, 2459a (4); 2468 (7); 3296 (30). Balegno 1191 (37). Bang 1215* (30). Basualdo 1876 (4); 2546 (23); 2658 (16); 3485a (13). Beck 5373 (10). Bernardello y Galetto 800 (10). Bernardi 18720 (4); 18891 (4); 19330 (4); 20142 (8); 20202 (34); 20335 (21), 20425 (22); 20457 (8). Bertoni 1168 (20); 1378 (7); 2433 (20); 2513, 4024 (4). Billiet y Jadin 3057 (15); 3123 (34); 3126 (37). Biurrun 584 (37); 1372 (12). Blanchet s.n.* (7); 2575* (1); 2979* (13). Bordas 3748 (32). Bordas y Schmeda 4093 (32). Borsini 613 (30). Botta 138 (34). Brizuela 456 (37); 927 (34); 1132, 1266 (12). Brooke 5586* (19); 5677* (13). Browne s.n.* (7); 2007 (19). Bruch y Carette 24 (12). Brunner 1442 (14); 1534 (4). Buchtien 1409* (3). Buratovich 635 (34). Burkart 5328 (37); 8498 (36); 12528 (34); 12531 (12); 13368 (36); 13958 (34); 14171 (2); 14280 (2); 14443 (25); 14603 (23); 20647 (36); 30640 (19).

Caballero Marmori 395 (30). Cabrera 7192 (36); 11995, 12072, 15515 (36); 16761 (21); 21719 (22); 26314 (34); 27112, 27228 (31); 27954 (26); 30759 (37); 31312 (18); 32149 (26); 32659, 34155 (24). Cabrera y Sáenz 29211 (4). Carter s.n. (10). Castellanos s.n. (15); (36). Claussen s.n.* (35). Covas 1102 (36). Cristóbal 340 (22); 442 (12). Cuezzo y de la Sota 1527 (23). Chamisso s.n.* (5). Charpin y Ramella 21485 (34); 21610 (6); 21733 (22); 21742 (6). Chodat s.n. (20).

de la Sota 96 (18); 1138 (15). De Marco 10654 C (4). Degen 1032 (4); 1522 (23); 1611 (23); 3280 (6). Degen y Mereles 3250 (8). Deginani 1135 (38); 1320 (5); 2080 (5). Descole 3187 (7). Di Lullo 27 (34). Díaz 10191 (33). Diers 46 (34); 225 (21). Duarte 1705* (7). Duarte y Pereira 1927* (15). Duré y Brunner 428 (33).

Echegaray s.n.* (12); s.n. (36). Eyerdam y Beetle 22275 (19).

Fabris 7302 (30). Fernández 144 (23). Fernández Casas 4114 (14). Fernández Casas y Molero 5855 (4); 6113b (32). Fernández Casas et al. 7516 (20). Ferrucci 758 (16). Fiebrig s.138 (10); 356 (20); 567, 888 (32); 916 (16); 1269 (20); 1423 (7); 4030 (20); 4103 (1); 4406 (9); 4433 (32); 4473 (9); 4662 (4); 4688 (7); 4811 (13); 4813 (38); 4967 (7); 5074 (10); 5730, 5826 (5); 5929 (25); 5934 (32); 6040 (23); 6081 (7); 6173 (23); 6174 (4). Fortunato 5880 (17); Fortunato y Palese 2970 (35). Frenguelli 128 (14).

Galetto 186 (33). Giardelli 1173 (34). Gillies s.n.* (12); s.n.* (36). Glaziou 13073* (13); 13076* (1); 21876* (28). Guaglianone 454 (20); 680 (8); 726 (4).

Hahn 787 (10); 1530 (35); 2481 (30). Hassler 138, 916, 1089*, 1138 (16); 1579, 1593 (4); 1650 (10); 1907 (2); 1936* (32); 2135 (38); 2754 (8); 2755* (10); 2962 (2); 2977 (30); 3016 (4); 3017 (32); 3053, 3057 (16); 3174 (30); 3508 (20); 3740 (32); 3920 (7); 4889 (20); 5108 (2); 5207 (4); 5719 (32); 5984 (20); 5985 (7); 6476 (16); 6813, 6813a, 7106 (2); 7560, 7624 (20); 7633 (29); 7749 (32); 7834, 8003 (9); 8160, 8160a (20); 8423, 8423a (28); 9271 (2); 9568* (38); 11105 (4); 11701 (30); 11740 (4); 12458 (32); 12530 (16). Hayward 1444 (20). Herrera 232 (18). Hicken 12911 (20). Hieronymus y Niederlein 46* (31); 140 (12); 546* (31). Hilgert 759, 766 (3). Hunziker, A. 1869 (31); 4708 (37); 4721 (12); 8947 (36); 9810 (34); 10068 (36); 10985, 12322 (12); 13915, 14691 (37); 14792 (34); 15096 (12); 15313, 16647 (34); 21843 (36); 22141 (21); 22457 (37); 22674 (36); 22854, 22863 (31); 25229 (34). Hunziker, A. y Caro 13560*, 13562 (17); 13618 (34). Hunziker, A. y Cocucci 16388 (12). Hunziker, A. y Maldonado 16245 (17). Hunziker, A. y Subils 24951 (37). Hunziker, J. 950, 959 (11); 10891 (23). Hunziker, J. y Gamerro 11669 (21).

Iudica y Ramadori 354 (3).

Jörgensen 698 (2); 982 (36); 2332bis (10); 2335 (20); 2336 pp (30); 2336 pp, 2337 (8); 2336bis (30); 2338 (15); 2832, 3278, 3796 (7); 4237 pp (20); 4237 pp (29); 4303 (32).

Kerr 108* (10). Kiesling 1262 (37); 3013 (17); 4345, 4718, 5823 (36); 5012 (12); 5562 (18); 5618 (7); 5838 (34); 5844 (37); 6402 (31); 6410 (36); 6780 (31); 6783 (37); 8961 (12). Krapovickas 1086 (1); 12328 (32); 12525 (32); 14312 (7); 15021 (25); 15161 (25); 17978 (25); 21611 (25); 45995 (9). Krapovickas y Cristóbal 11812 (7); 11889 (10); 44290 (37); 46675 (34). Krapovickas et al. 13889 (1); 13896 (20); 14227 (4). Kuntze s.n.* (1); s.n.* (13), s.n.* (16), s.n.* (15), s.n.* (19), s.n.* (29), s.n.* (32). Kurtz 13260 (21); 14223* (21).

Lanfranchi 300* (20). Legname y Cuezzo 5514 (36); 5970C (18); 8463 (24); 8564c* (26); 9707 (26). Legname s.n. (34); 3387 (37); 5372 (22); 5967 (7); 6052, 6857 (15); 7043 C (26); 7264 (36); 7521 (36); 8893 (37); 9005 (36); 10151 C (30). Lillo 4417 (22); 6082, 7894 (12); 8087* (22); 10520 (30). Legname y López 8704 (15). Linden 1633* (7). Lorentz s.n.* (34); 12* (37); 118* (36). Lorentz y Hieronymus 301* (34). Luschnath s.n.* (5).

Macedo 952* (28); 1123* (13); 1617* (28). Malme s.n.* (36); 3029* (8). Malvárez 675 (36). Mandon 297* (24). Maranta 295 (27). Marmol 8734 (19). Martínez Crovetto 3376 (26). Martius s.n.* (1), s.n.* (4), s.n.* (5), s.n.* (19), s.n.* (39). Maruñak 678 (4). Mathews 3152bis* (9). Maximilianus Vied* (7). Mereles 1198 (4); 1208 (7); 2054 (14); 2430 (20); 2795 (6); 3270 (7); 3904 (4). Mereles y Degen 5190 (37); 5563 (10). Mereles y Ramella 2795 (6). Meyer s.n. (37); 2094 (7); 2998 (15); 3797 (20); 8570 (36); 8669 (15); 9067 (30); 10198 (36); 10281 (20); 12195, 12789 (37); 13853, 15125* (24); 16102 (20); 16235 (10); 16416 (18); 16492 (34); 21829 (12). Molas 1073 (27). Montes 841 (25); 7157 (7); 9806, 10933, 15762, 16162, 16383 (25). Moore 667* (29); 941* (20); 1047* (6). Morel 161 (20); 605 (7); 1719 (10); 7182 (4); 7190 (7). Morello s.n. (34); 966 (24); 16936 (20). Morong 200a (4); 435 (20); 667* (32); 706* (30); 1031 (20); 1538* (10). Morrone 695 (38); 3087 (33). Mroginski 242 (4). Múlgura 675, 738 (17); 927 (15); 1039 (20); 1079 (24); 1891 (5). Muller 172 (34).

Nicora s.n. (SI 17632), s.n. (SI 18623) (37); s.n. (SI 18656) (12); 1793 (12). Niederlein 1776 (11). Novara 3502 (15); 5826 (18); 8055 (24); 8532 (22). Novara y Charpin 10344 (19). Novara y Ternel 10284 (15). O'Donnell 5368 (18). Ortiz 1280 (23). Osten y Rojas 8978 (16).

Palmer s.n. (32). Parodi 8511 (10). Pedersen 3132 (32); 5994 (7); 10148 (32). Peirano 9021 (37); 10453 (33). Pierotti s.n. (12); 83 (15); 4204 (4); 5131 (34); 6620 (30); 7172 (22). Pire 3813 (36). Poeppig s.n.* (7). Pohl s.n.* (23); s.n. (35); 196* (5); 1849* (1); 1989* (14). Porta 39 (23).

Quarín 367 (20). Quarín et al. 1510 (20).

Ragonese y Piccinini 9408 (36). Reales 94 (4); 1043 (37); 1055 (36). Reic 605 (34). Riedel s.n.* (7); s.n.* (20); s.n. (39); 88* (14); 1983* (23). Rizzini y Irene 21* (4). Rocha 108 (22). Rodriguez 288 (25); 597 (37); 755 (7); 789 (5); 1045 (26). Roig 8053 (21). Rojas 81 (10); 155 (15); 362 (7); 664 (4); 2198 (29); 2199 (20); 2631 (29); 2755 (10); 2818 (15); 2930 (20); 8070 (30); 9718 (38); 10152 (28); 10402 (13); 10463 (30); 10688 (5); 10864 (13); 10929 (1); 13842 (22). Romanczuk 188 (2). Ruiz Huidobro 2128 (4); 3250 (20); 3348 (20); 3714 (7); 4249 (4); 4301 (4); 4876 (2). Ruiz Leal 11819 (12); 22103 (21). Rusby 1117* (32); 1421* (20).

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Apéndice 3

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PLANT DIVERSITY OF THE CAPE REGION OF SOUTHERN AFRICA[1]

Peter Goldblatt[2] *and John C. Manning*[3]

Abstract

Comprising a land area of ca. 90,000 km^2, less than one twentieth (5%) the land area of the southern African subcontinent, the Cape Floristic Region (CFR) is, for its size, one of the world's richest areas of plant species diversity. A new synoptic flora for the Region has made possible an accurate reassessment of the flora, which has an estimated 9030 vascular plant species (68.7% endemic), of which 8920 species are flowering plants (69.5% endemic). The number of species packed into so small an area is remarkable for the temperate zone and compares favorably with species richness for areas of similar size in the wet tropics. The Cape region consists of a mosaic of sandstone and shale substrata with local areas of limestone. It has a highly dissected, rugged topography, and a diversity of climates with rainfall mostly falling in the winter months and varying from 2000 mm locally to less than 100 mm. Ecological gradients are steep as a result of abrupt differences in soil, altitude, aspect, and precipitation. These factors combine to form an unusually large number of local habitats for plants. Sandstone-derived soils have characteristically low nutrient status, and many plants present on such soils have low seed dispersal capabilities, a factor promoting localized distributions. An unusual family composition includes Iridaceae, Aizoaceae, Ericaceae, Scrophulariaceae, Proteaceae, Restionaceae, Rutaceae, and Orchidaceae among the 10 largest families in the flora, following Asteraceae and Fabaceae, as the most speciose families. Disproportionate radiation has resulted in over 59.2% species falling in the 10 largest families and 77.4% in the largest 20 families. Twelve genera have more than 100 species and the 20 largest genera contribute some 31% of the total species. Species richness of the Cape flora is hypothesized to be the result of geographic and parapatric radiation in an area with a mosaic of different habitats due to local soil, climate, and altitudinal differences that combine to produce steep ecological gradients. Also contributing to the diversity has been a relatively stable geological history since the end of the Miocene that saw the establishment of a semi-arid and extreme seasonal climate at the southwestern part of southern Africa.

Key words: floristics, Mediterranean-type climate, phytogeography, plant diversity, southern Africa, speciation.

Situated at the southwestern tip of the African continent between latitudes 31° and 34°30′S (Fig. 1), the area that has come to be called by biologists the Cape Region has a flora, and to a lesser extent a fauna (Stuckenberg, 1962), that is so sharply distinct from that of the land immediately adjacent to it that it has impressed naturalists from the time of its discovery by European explorers in the 16th century. Indeed, the floristic characteristics of the Cape Region are so unusual that it has sometimes been regarded as one of the world's six floral kingdoms (e.g., Good, 1974; Takhtajan, 1986). There are, however, no objective criteria for distinguishing such "floral kingdoms," and recognition of a Cape Floral Kingdom is not universal. We use the neutral term "floristic region" here simply for convenience.

Comprising a land area of ca. 90,000 km^2, less than 5% of the total area of the southern African subcontinent (Goldblatt, 1978, 1997), the Cape Floristic Region (CFR) is one of the world's most botanically diverse regions. An estimated 9030 species of vascular plants (ferns and other vascular cryptogams, gymnosperms, and flowering plants), the majority of which, some 8920 in total, are flowering plants, occur there, almost 69% of which are endemic (figures based on Goldblatt & Manning, 2000, but reflecting taxonomic changes made since the completion of that work). Thus, the flora of the Cape Region comprises 44% of the estimated 20,500 species that occur in all of southern Africa (Arnold & de Wet, 1993; de Wet, pers. comm.). The level of species richness is notable, particularly in Africa, the tropical flora of which is relatively depauperate, but is remarkable for the world's temperate zone, comparing favorably with species richness for areas of comparable size in the wet tropics rather than for areas of temperate climate.

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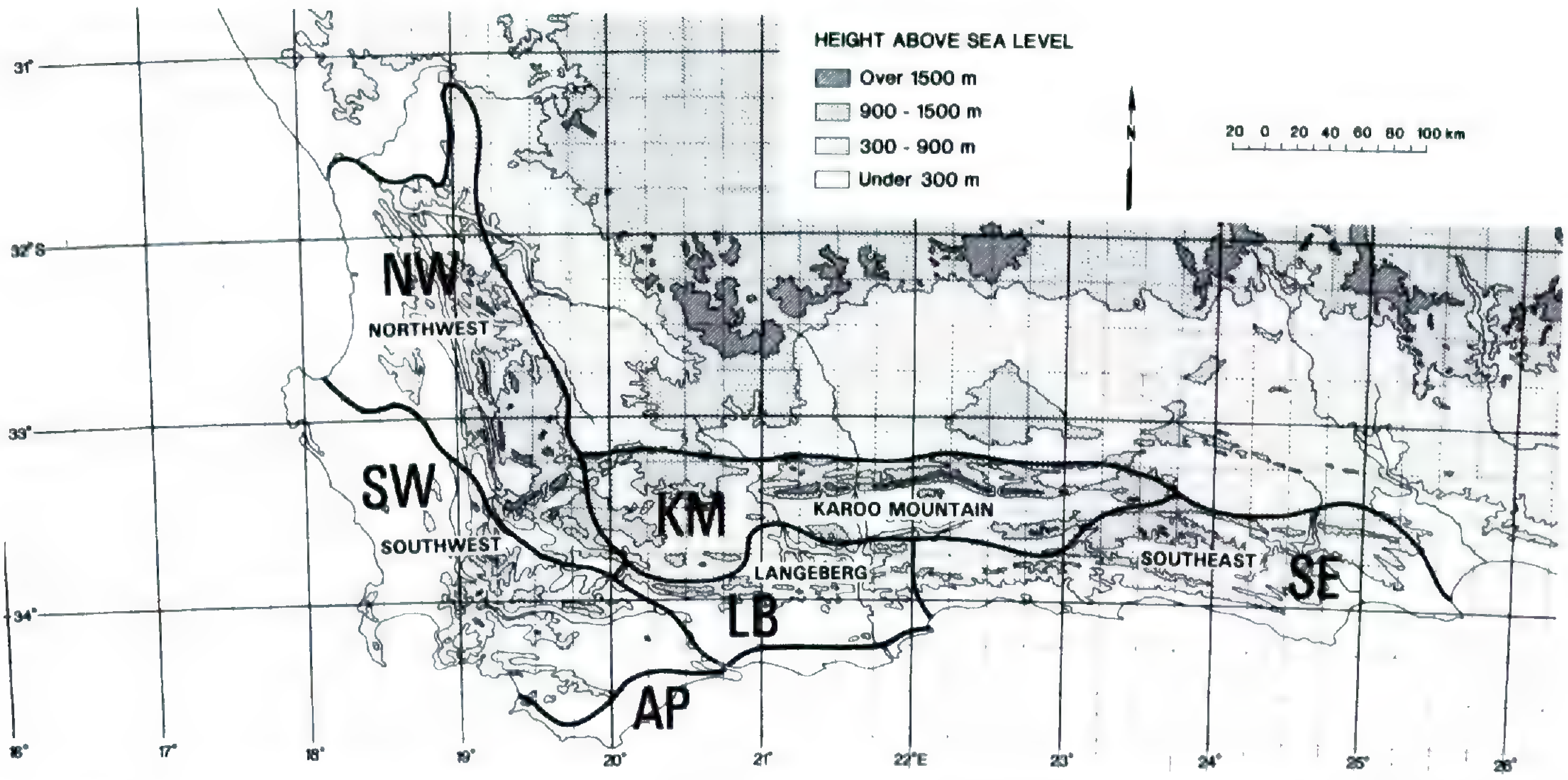

Figure 1. The Cape Floristic Region, showing relief, with the phytogeographic centers marked (from Goldblatt & Manning, 2000). Abbreviations: AP, Agulhas Plain; KM, Karoo Mountain; LB, Langeberg; NW, Northwestern; SW, Southwestern; SE, Southeastern.

Not only is the plant species richness of the Cape flora exceptional, but its familial and generic composition is remarkable (Bond & Goldblatt, 1984; Goldblatt, 1997; Goldblatt & Manning, 2000). Unexceptionally for a region of fairly dry climate, the largest families are the Asteraceae and Fabaceae, together comprising some 20% of the total species. The families next in size, however, are not matched in any other flora—nowhere else in the world do Iridaceae, Aizoaceae, Ericaceae, Proteaceae, and Restionaceae assume such numerical significance, except in some parts of Australia where Proteaceae and Restionaceae are also unusually well represented. Other peculiarities of the Cape flora are the dominance of fine-leaved sclerophyllous shrubs, the paucity of trees, and a remarkably large number of geophytes, here defined as seasonal herbaceous perennials with bulbs, corms, tubers, or prominent rhizomes (thus excluding shrubs and subshrubs that resprout from a woody caudex, usually after fire). Such geophytes, especially numerous among the monocots (notably, in order of importance, Iridaceae, Orchidaceae, Hyacinthaceae, and Amaryllidaceae), also include many species of *Oxalis* (Oxalidaceae) and *Pelargonium* (Geraniaceae) as well as other eudicots. Geophytes as so defined comprise slightly more than 17% of the species in the CFR. Conversely, the Cape flora has a surprisingly low proportion of annuals for an area of largely semi-arid climate. Approximately 6.8% of the species are annuals, which is a striking contrast to California (30% annuals) or Chile (nearly 16% annuals) (Kalin Arroyo et al., 1994), areas of comparable latitude and climate. Both geophytes and annuals are primarily adapted to seasonally dry climates and escape the time of year unfavorable for growth by retreating to underground storage organs or by ensuring continued survival only by the production of seeds.

The compilation of a synoptic flora of the Cape Region (Goldblatt & Manning, 2000) replaces earlier vegetational analyses based on the work of Bond and Goldblatt (1984), now very much out of date. Statistics presented here are taken from Goldblatt and Manning (2000), with minor modifications reflecting taxonomic changes in press or published since its completion. Familial and ordinal taxonomy is that recommended by the Angiosperm Phylogeny Group (APG, 1998). Changes in the CFR made since this synoptic classification was published are recognition of Veronicaceae (now including Plantaginaceae and several genera previously of Scrophulariaceae), enlargement of Stilbaceae to include non-Cape genera, the reduction of Achariaceae in Flacourtiaceae, and Prioniaceae in Thurniaceae, and the transfer of *Hyaenanche* from Euphorbiaceae to Picrodendraceae (= Pseudanthaceae) (Olmstead et al., 2001, and pers. comm.; Chase et al., 2000; Savolainen et al., 2000). Tamaricaceae, represented by one species of *Tamarix*, was omitted in error from the account of the flora. These changes are represented in the revised familial statistics.

PHYSICAL CHARACTERISTICS

LANDSCAPE AND CLIMATE

Mountain belts of the Cape Region are not particularly high, generally 1000–2000 m in elevation, and although the peaks are well below a truly alpine zone at the latitude of the Cape region, they are high enough for winter freezing to be a factor affecting the vegetation. The mountains are rugged, and cliffs and exposed rock are evident everywhere. The rugged topography and vertical landscape amplify the effects of local climatic variation with the result that the mountains offer a greater diversity of habitats than are present in the lowlands.

The climate is largely mediterranean, and strictly so in the west, although the eastern half of the CFR receives substantially more summer precipitation. Rain thus falls mainly in the winter months and while summers are hot and dry, they are relatively less so in the east. In areas of low total rainfall, the average monthly precipitation distributed in the summer months may be higher, notably in the Little Karoo, but due to more favorable precipitation/evaporation (P/E) ratios effective rainfall is still mainly in the winter. South-facing mountain slopes benefit from summer moisture in the form of rain or fog from the southeast trade winds. The narrow coastal plain in the Knysna area, which has a comparatively equable climate and high rainfall, supports an evergreen, broad-leaved forest. Likewise, sheltered valleys and locally wet sites throughout the region, affording higher P/E ratios, support forest vegetation.

Local variation in rainfall is particularly pronounced in mountainous areas, and this is important when precipitation is orographic. Mountain slopes facing prevailing winds receive considerably more precipitation than those in the lee. Rainfall patterns in the Cape Region show dramatic variation in quantity, dropping from 2000 mm per year on the high mountains of the ranges immediately facing the coast, to less than 200 mm on the leeward slopes of the interior ranges. Mosaic effects of soils across the entire region are thus complicated by variation in precipitation from the coast to the interior, as well as changes in seasonality from the west to the east. In addition, elevation and aspect affect precipitation depending on the direction of moisture-bearing winds. The eastern and western parts of the CFR are considered to be under fundamentally differing climatic controls, probably a long enduring pattern that has affected the evolutionary histories of the areas and, hence, resulting in their distinctive floras and faunas (Cowling et al., 1999).

The number of ecological niches available to plant life is multiplied by soil differences, and this is particularly pronounced as precipitation levels drop. With ample rain the effect of soil on vegetational composition is less prominent. Rainfall is limiting almost throughout the region, however, and vegetation varies conspicuously with soil and available moisture. Climatic gradients are steep, although perhaps not more so than in most other areas of mediterranean climate, but the effect may be compounded in the Cape Region by soil diversity. Different soil types in the Cape Region support characteristic vegetation types depending on associated levels of precipitation. Forest vegetation is typical of deeper soils and sites where precipitation is high and fairly evenly spread throughout the year. As soil qualities change and precipitation becomes lower or more seasonal, forest gives way to shrubby or herbaceous vegetation types. On sandy soils, forest yields to a sclerophyllous vegetation (fynbos) in which species diversity decreases and composition changes until rainfall minimums reach about 300–250 mm p.a. when a succulent shrubland becomes dominant. On clay soils forest gives way to fynbos and then to the characteristic renosterveld, a shrubland dominated by shrubby, microphyllous Asteraceae. At precipitation levels below 100 mm p.a. renosterveld is increasingly dominated by succulent perennials. The dissected landscape ensures that broad sweeps of one vegetation type are isolated from others by habitats that will not support their growth. The mosaic of different soil types alone contributes to increasing diversity, but the peculiar nature of nutrient-poor soils may result in more pronounced effects on plant diversity, plant dispersal, and hence gene flow.

GEOLOGY AND SOILS

Over most of its surface the Cape Region is covered by soils derived from rocks of pre-Carboniferous age (King, 1962), thus more than 400 mya (Fig. 2). Most of these rocks comprise part of the Cape System, an ancient Devonian–Ordovician series of sediments consisting of alternating layers of largely quartzitic sandstones (the Table Mountain and Witteberg Groups) or fine-grained shales (the Bokkeveld Group). During the Jurassic the land surface was folded and warped as Antarctica separated from the south coast of southern Africa and South America rifted away from the west coast. The folds consistently run parallel to the coasts, resulting in a series of east-west trending mountain ranges in the southern half of the Cape Region and north-south trending ranges in the west.

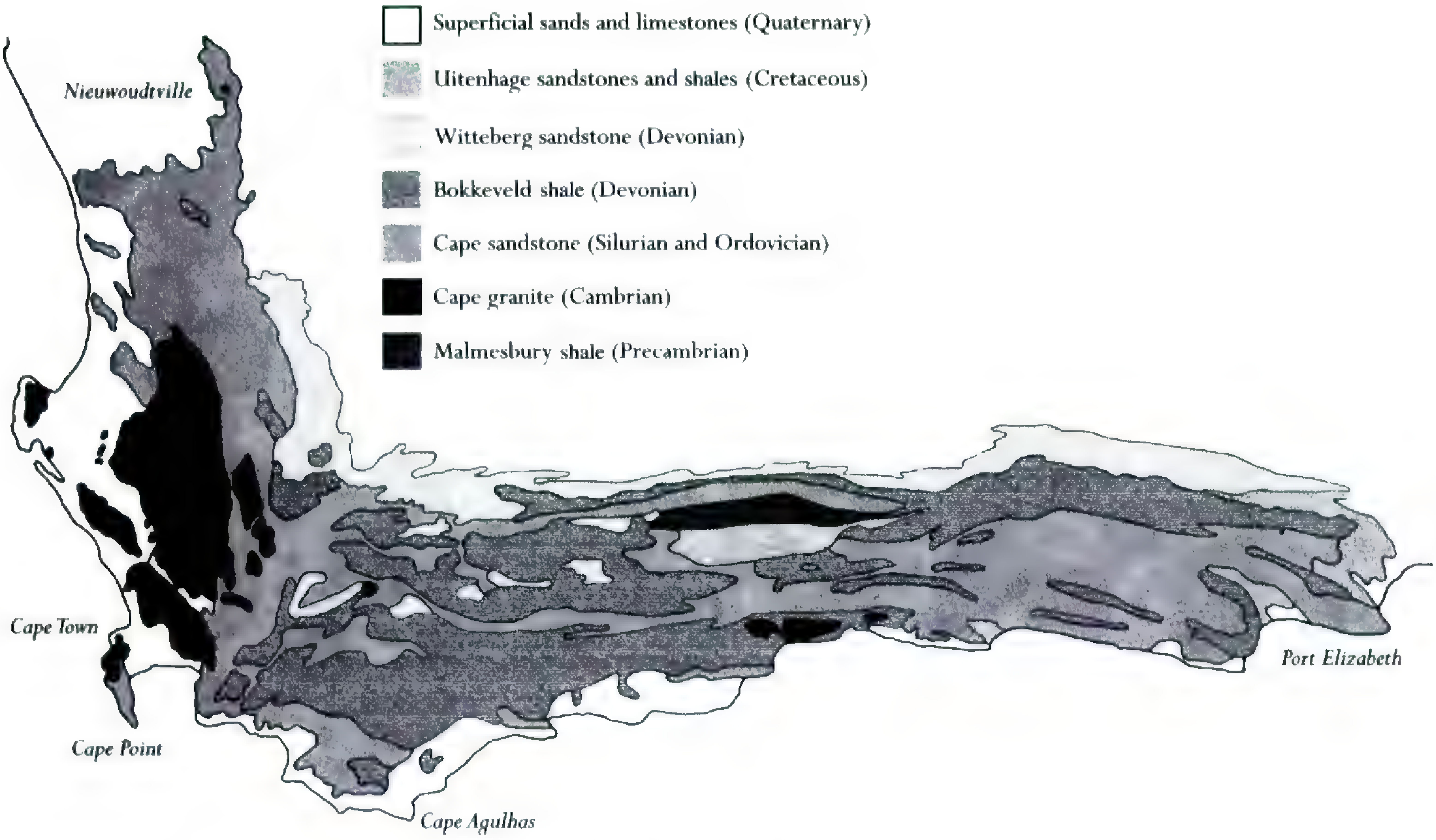

Figure 2. Geology of the Cape Floristic Region (adapted from Cowling, 1992).

Differential weathering of the components of the Cape System has yielded two fundamentally different soil types, coarse-grained sandy soils, poor in essential plant nutrients, and richer, clay soils of nutrient-intermediate status (Groves et al., 1983). At the low precipitation levels that are usual in the Cape Region, these factors become so limiting that these soils support markedly contrasting vegetation. Apart from variation in nutrient status, the soils depart significantly in their structure and water-retention properties. Erosional patterns differ on the two rock types, and the result is that the mountains consist primarily of sandstone rocks and the valleys of shale. Where folding or faulting have been severe, more ancient rocks of the Precambrian Malmesbury Group are exposed. These are largely shales that give rise to clay soils of the same type as do the shales of the Cape System. Granitic schists are locally exposed in deep valleys and along the west coast, and limestones, mainly of Tertiary age, are exposed near the coast where they are extensive only along the southern coast from the Agulhas Peninsula east to Mossel Bay. The coastal plain includes areas with aeolian sandy soils derived from reworking of Cape Sandstones. Since these major episodes of folding and rifting in the Mesozoic, only erosional forces have had a major impact on the Cape landscape, modified only slightly by minor uplift, associated with coastal downwarping in the mid to late Tertiary (King, 1962). Moving from the coastal plain to the interior, the resultant landscape is a mosaic of coastal limestones and deep sands, or valleys with clay soils alternating with mountain ranges of nutrient-poor sands. Local faulting has added a secondary component of islands of one rock type embedded in another. Both the nutrient-poor and nutrient-intermediate soils favor the development of a fairly uniform, sclerophyllous, shrubby vegetation that is fire-adapted (see discussion under Diversity).

WINTER-RAINFALL AND CLIMATIC STABILITY

How important to the flora is the current mediterranean climate that prevails over most of the Region? The vegetation of the Cape Region prior to the establishment of a winter-rainfall climate was very different from that now found there. Evergreen forest has been decreasing since the middle of the Tertiary, and its diversity has dropped dramatically since the mid Miocene, some 16–14 mya, as well (Coetzee, 1993). Families such as Arecaceae, Casuarinaceae, Chloranthacaeae, Sarcolaenaceae, and Winteraceae, no longer found on the African mainland but still extant in Madagascar, were present in the Cape Region at least until the mid Miocene (Coetzee & Praglowski, 1984; Coetzee & Muller, 1985). In addition, early to mid Miocene deposits on the Cape west coast indicate a fauna adapted to forest and woodland (Hendey, 1982).

The establishment of the cold Benguella Current along the west coast of southern Africa in the Mio-

cene, with its cooling and drying effects, was probably the single most important influence affecting vegetation change in the subcontinent. Summer drought became increasingly severe in the west as this current strengthened as a result of the spread of the Antarctic ice sheet at the end of the Miocene, ca. 5.5 mya. Even in the later mid Miocene, however, there was a fairly rich subtropical flora replete with palms (Coetzee & Rogers, 1982) near Saldanha Bay, on the west coast of the Cape Region in an area that today supports a largely treeless, succulent or sclerophyllous shrubland. No palm species occur today in the CFR. Faunal remains suggest that by the late Miocene the once widespread forest and woodland were being replaced by more open savanna (Hendey, 1982). It was probably not until after the beginning of the Pliocene, i.e., less than 6 mya, that the present Cape flora could be distinguished, although elements of that flora are recognized in Oligocene pollen cores taken within the Cape Region and nearby (Scholz, 1985). It seems clear that climatic change, including increased summer drought and lower overall rainfall, was the driving force for vegetational change in southern Africa into the Pliocene.

Although post-Pliocene changes in climate of the Cape Region are poorly documented, the climate appears to have been relatively stable. In comparison with southern Europe, North America, and southern South America, all of which experienced cycles of extreme climatic fluctuations with periods of mild climate alternating with extreme cold and dryness (Villagrán, 1994), the climate of the Cape Region appears to have been relatively stable throughout the Quaternary. Whereas in central Chile, southern Europe, and North America mountain glaciers developed and winter temperatures must have fallen to levels that large portions of their floras could not tolerate, the Cape appears to have merely undergone cycles of drier and cooler alternating with wetter and warmer conditions. The ameliorating affects of large oceans to the south and west would have prevented the extreme conditions that result in major extinction events. Although no glaciers developed, there is evidence of colder climates in the past (Deacon, 1979) consistent with a temperature depression of the order of 5°C at the latitude of the Cape Region.

The data of Meadows and Sugden (1991) are among few documenting the history of the Cape flora over the past 20,000 years. Their pollen profiles from the Cedarberg Mountains in the northwestern part of the CFR show no vegetational changes comparable to those known for Chile (Villagrán, 1994) or California (Raven & Axelrod, 1978). Instead, there seems to have been a series of subtle shifts in conditions that favored one community type over another in the 14,600 years covered in their sampling. The Cedarberg data are especially notable because that range lies at the northern, more arid end of the Cape Region, an area that is therefore particularly sensitive to climatic change. In contrast, the somewhat older fossil wood assemblages from Elands Bay Cave on the west coast of the CFR (Cowling et al., 1999) document a shift from xeric to mesic thicket and fynbos and then to afromontane forest at 18,000 BP, indicating higher moisture conditions in the west during the Last Glacial.

In the southern Cape the lowering of sea levels as much as 120 m below present levels at times during the Pleistocene resulted in the extension of the coastal plain off the southern coast of Africa. The vegetation along the coast at this time was probably grass-dominated, and it supported the dominant alcephaline and equid fauna (Klein, 1977). Even today, the vegetation on clay soils of this area has a large grass component.

Floristic Composition

Major Families and Genera

The Asteraceae, usually the largest family in floras of arid to semi-arid regions, are also the most speciose family in the Cape flora, with 1036 species (Table 1). Additions to several genera of Fabaceae since the flora was last documented (Bond & Goldblatt, 1984) now make this family the second largest in the flora (previously believed to be fourth largest), which is also unexceptional, as Fabaceae are well developed in most parts of the world. However, the huge contribution made by Iridaceae, Aizoaceae, and Ericaceae, next in numbers of species (Table 1), is a unique aspect of the flora (and consequently of the southern African flora as a whole). Scrophulariaceae, Proteaceae, and Restionaceae follow in importance, showing a pattern, described in more detail by Goldblatt and Manning (2000). Aizoaceae, with its huge southern African representation of Mesembryanthemoideae, are probably the second largest family in the southern African flora (Goldblatt, 1978) and appear to be the largest family in the Namaqualand–southwestern Namibia region (R. Cowling, pers. comm.) that lies to the north of the CFR and also has a winter-rainfall and summer-dry climate. This arid zone has such strong floral affinities to the Cape flora that the inclusion of Namaqualand–southwest Namibia in the CFR to comprise a Greater Cape flora has been given serious consideration (Bayer, 1984; Jürgens, 1991, 1997). The relationships of the extended Namaqua-

Table 1. Ranking of the 20 largest families in the Cape Flora Region as indicated by species number. Family circumscriptions reflect the recommendations of the Angiosperm Phylogeny Group (1998). These families contribute 6989 species to the flora, or 77.4% of the total.

	Family	Total species	Number endemic (% of total species)	Total genera (number endemic)	Species/genus
1.	Asteraceae	1036	655 (63.2)	121 (33)	8.6
2.	Fabaceae	761	629 (82.7)	37 (6)	20.6
3.	Iridaceae	677	540 (79.8)	28 (6)	24.2
4.	Aizoaceae	659	524 (79.5)	76 (18)	7.5
5.	Ericaceae	657	637 (96.9)	1 (0)	657
6.	Scrophulariaceae	414	297 (71.7)	33 (7)	12.5
7.	Proteaceae	329	319 (97.0)	14 (9)	23.5
8.	Restionaceae	318	294 (92.5)	19 (10)	16.7
9.	Rutaceae	273	257 (94.1)	15 (6)	18.2
10.	Orchidaceae	227	138 (60.8)	25 (2)	9.1
11.	Poaceae	207	80 (38.6)	61 (3)	3.4
12.	Cyperaceae	206	101 (49.0)	29 (4)	7.1
13.	Hyacinthaceae	191	83 (43.5)	14 (0)	13.6
14.	Campanulaceae	183	140 (76.5)	13 (6)	14.1
15.	Asphodelaceae	157	81 (51.6)	8 (0)	19.6
16.	Geraniaceae	157	91 (58.0)	3 (0)	52.3
17.	Polygalaceae	141	122 (86.5)	3 (0)	47.0
18.	Rhamnaceae	137	127 (92.7)	5 (1)	27.4
19.	Crassulaceae	134	35 (26.1)	5 (0)	26.8
20.	Thymelaeaceae	125	94 (75.2)	4 (1)	31.3
		Σ = 6989	5244 (77.0)	514 (112)	

land flora (or Succulent Karoo Region) seem unquestionably closer to the Cape flora in its traditional sense than to the flora of the summer-rainfall karoo (Nama-Karoo Region) although their common boundary is not clearly fixed and there is evidence for its east–west shift in the past (Jürgens, 1991).

The large numbers of species of Proteaceae and Restionaceae, seventh and eighth largest families, respectively, are another striking feature of the flora. The importance of Ericaceae, Proteaceae, and Restionaceae both in terms of biomass and species diversity is widely appreciated, but the huge number of species of Iridaceae, predominantly a family of herbaceous, seasonal geophytes, is especially notable. Nowhere else in the world does this family comprise such a significant floristic component. Indeed, the adaptive radiation of Ericaceae and Iridaceae in the Cape flora is one of its most striking features. The diversification of Ericaceae, Proteaceae, Restionaceae, and even Cyperaceae, is closely associated with the impoverished sandstone soils of the Cape mountain ranges, and these families are poorly represented on other soils. The massive radiation of Fabaceae and Iridaceae shows no such correlation. Although the wealth of Scrophulariaceae, sixth largest family in the Cape flora, seems remarkable in a world context, the family is also well represented across Africa, especially in the floras of drier areas (Maggs et al., 1998). In the Cape flora Scrophulariaceae contribute 166 species to the annual flora, far more than does the next most important family, Asteraceae, with 138 annual species. As circumscribed for the Cape flora (Goldblatt & Manning, 2000) Scrophulariaceae do not include the parasitic and hemiparasitic genera now referred to Orobanchaceae (APG, 1998) but, nevertheless, it remains a major family in the flora. Rutaceae, ninth largest family, are also a surprising aspect of the Cape's floristic composition. Over 95% of the 273 species of Rutaceae there are small shrublets belonging to the tribe Diosmeae, most members of which are restricted to the Cape flora, and reflect the large numbers of shrub species in the flora. The wealth of Polygalaceae, Rhamnaceae, and Thymelaeaceae, 17th, 18th, and 20th in size, respectively (Table 1), likewise exemplify the importance of the shrubby habit in the Cape flora.

Poaceae are comparatively poorly represented in the Cape flora. Although they are the third largest family in the flora in number of genera (Table 1), they are only 11th in size in total species, with fewer representatives than Restionaceae and barely more than Cyperaceae, the two other families generally that occupy similar habitats. This situation is

Table 2. Endemic families of the CFR. Note that the characteristic and nearly endemic family Bruniaceae has 11 genera and 61 endemic species of a total 64 in the family and is not included here, its range extending eastward to southern KwaZulu-Natal. In addition, Olmstead et al. (2001) have proposed enlarging Stilbaceae to include non Cape genera rendering it no longer endemic.

Family	Number of genera	Number of species
Penaeaceae	7	23
Stilbaceae s. str.	5	14
Grubbiaceae	1	3
Roridulaceae	1	2
Geissolomataceae	1	1
Totals	15	43

paralleled only in southwestern Australia but contrasts sharply with adjacent southern Africa where Poaceae are prominent and diverse. Poaceae are the largest family in the flora of Namibia (Maggs et al., 1998) and one of the five largest in southern Africa excluding the CFR (Goldblatt, 1978).

Although 150 families of seed plants and another 23 of ferns and other vascular cryptogams are represented in the flora, remarkably few account for the bulk of the species. While 23 families in the flora have over 100 species, only 12 have over 200 species. In contrast, 38 families have just one species each. The largest 10 families account for 5351 species, well over half the total 9030 in the flora, and the largest 20 families account for 6989 species, over 77% of the flora (Table 1).

ENDEMIC FAMILIES

The unique floristic composition of the Cape Region, with its high representation of Ericaceae, Iridaceae, Proteaceae, and Restionaceae (Table 1), is emphasized by the presence of several families that are endemic or nearly so. The endemic families are all eudicotyledons of diverse affinity and relatively low evolutionary specialization (Table 2). The largest is Penaeaceae (Myrtales), followed by Grubbiaceae (Cornales), Roridulaceae (Ericales), and Geissolomataceae (together with Ixerbaceae and Strasburgeriaceae, sister to Crossosomatales) (classification following APG, 1998). Based on a molecular clock calibrated using 135 mya for the divergence of the eudicot lineage (V. Savolainen et al., 2000, and unpublished data), Penaeaceae may have diverged 20 mya from its sister clade, the African Oliniaceae plus the Neotropical Alzateaceae, while Roridulaceae diverged from Ericaceae, its closest relative (Savolainen et al., 2000), ca. 48 mya. Geissolomataceae appear older, having diverged perhaps 55 mya from Ixerbaceae plus Strasburgeraceae. Grubbiaceae may have diverged from Cornaceae plus Hydrostachyaceae in the earliest Tertiary, 63 mya. We have no comparable data for the monotypic, near endemic monocot family Lanariaceae. Stilbaceae (including Retziaceae) (Lamiales) are provisionally regarded as a Cape endemic family, but if the changes to its circumscription suggested by Olmstead et al. (2001, and pers. comm.) are accepted, the family occurs across sub-Saharan Africa, Arabia, the Mascarenes, and Madagascar (see below).

Bruniaceae, one of the distinctive families of the Cape flora, are almost endemic. Of an estimated 64 species in 11 genera, just 3 species in 2 genera extend outside the confines of the Cape Region, 2 locally, and 1 as far east as southern KwaZulu-Natal. Bruniaceae are now thought to be the sister group to the order Dipsacales (Savolainen et al., 2000), perhaps meriting recognition at ordinal rank. The discovery of pollen matching modern Bruniaceae in early Tertiary and late Cretaceous (?Senonian) deposits in northern Namaqualand (S. E. de Villiers, pers. comm.), well to the north of the CFR, attest to considerable age for the family in southern Africa. The pollen record also accords with Savolainen's preliminary early Tertiary dating of the divergence between Bruniaceae and Dipsacales at about 57 mya (V. Savolainen, unpublished data).

Retziaceae (1 genus: 1 species) have often been considered an endemic Cape family (e.g., Bond & Goldblatt, 1984), although its affinities have long been in dispute (Goldblatt et al., 1979). DNA sequence analysis shows the genus nested in Stilbaceae (Bremer et al., 1994; Savolainen et al., 2000). Floral specialization for bird pollination appears to be the source of most of its distinctive features. The familial status of Stilbaceae is not in question, but Olmstead et al. (2001) included the Afro-Arabian *Nuxia* in tribe Stilbeae and added the Afro-Madagascan *Halleria* and the southern African tribe Bowkerieae to the family (previously Scrophulariaceae) rendering Stilbaceae no longer endemic to the CFR or even to southern Africa.

In contrast to the Cape Region, which alone has 5 (or more likely 4) endemic families, all of southern Africa perhaps has just 10 endemic families (9 according to the revised concept of Stilbaceae). In addition to those absolutely restricted to the Cape Region, the southern African endemic families are the eudicots Bruniaceae (ordinal position sister to Dipsacales, 11: ca. 64), Greyiaceae (Geraniales, 1: 3), and Rhynchocalycaceae (Myrtales, 1: 1); the

Table 3. Ranking by numerical size of the 20 largest genera in the CFR (endemic species number). An estimated 9030 species occur in the flora, of which 6208 are endemic (68.7%).

Erica	657 (637)	*Muraltia*	106 (100)
Aspalathus	272 (258)	*Gladiolus*	106 (86)
Pelargonium	148 (89)	*Selago*	100 (77)
Agathosma	143 (138)	*Crassula*	95 (26)
Phylica	133 (126)	*Disa*	92 (78)
Lampranthus	124 (118)	*Ruschia*	88 (79)
Oxalis	119 (94)	*Restio*	85 (82)
Moraea	115 (79)	*Leucadendron*	82 (79)
Cliffortia	114 (104)	*Helichrysum*	81 (34)
Senecio	110 (57)	*Thesium*	81 (35)

Total in largest 10 genera = 1935 spp. (21.4% of flora)
Combined total in largest 20 genera = 2851 spp. (31.6% of flora)

monotypic monocot genus *Lanaria* is also currently regarded as comprising its own family, Lanariaceae (Asparagales) (APG, 1998; Chase et al., 2000); and the cycad family Stangeriaceae (1:1). *Lanaria* is widespread in the Cape Region and extends outside its confines a short distance to the east. Aitoniaceae, Curtisiaceae, and Oftiaceae have at times been accorded recognition but they are no longer considered to be separate families. They are readily referable to Meliaceae (Pennington & Styles, 1975), Cornaceae (Xiang et al., 1993), and Scrophulariaceae (Goldblatt, 1979), respectively. Prioniaceae (Poales), treated as a family by Munro and Linder (1998) for the monotypic and largely Cape *Prionium,* and recognized by Goldblatt and Manning (2000) for the Cape flora, are now regarded as belonging to Thurniaceae (Chase et al., 2000). Behniaceae, described for the monotypic southern African *Behnia,* is an endemic southern African family according to Conran et al. (1997), although it is reported to occur in Zimbabwe. However, the status of Behniaceae is in question and it is likely to be subsumed in a more widely circumscribed Agavaceae (M. W. Chase, pers. comm.). Likewise, Achariaceae (Malpighiales, current name for Flacourtiales, 3:3) (Savolainen et al., 2000), two species of which also occur in the Cape Region, are often regarded as a southern African endemic family. The genera are, however, nested in Kiggelariaceae (Savolainen et al., 2000) and are regarded here as members of that family.

Genera

Some 944 genera of seed plants (or 990 genera of vascular plants), about half of those occurring in southern Africa, are represented in the Cape flora, of which some 160 or 16.3% are endemic (Goldblatt & Manning, 2000). The level of generic endemism is modest and reflects little of the unusual nature of the flora. The number of near-endemic genera (those of moderate size with just one or two species extending locally outside the Cape Region) is, however, dramatically high. The largest genus in the flora by far is *Erica,* with some 657 species (Table 3). Changes in the circumscription of *Erica* (Oliver, 2000) have now resulted in the inclusion of all the minor genera of southern African Ericaceae: Ericoideae, leaving *Erica* with over 7% of the species in the entire flora. It is unclear whether this remarkable pattern of speciation without generic diversification is associated with the relatively recent arrival of ancestral ericaceous stock in the CFR, or with adaptive radiation following the establishment of a semi-arid climate there. By comparison, the smaller families Proteaceae and Restionaceae appear to belong to old African (or even Gondwanan) groups, now poorly represented elsewhere in Africa, and they show the highest levels of endemism at the generic level. These two families plus Bruniaceae are the only non-endemic families that show greater than 50% generic endemism.

Aspalathus (Fabaceae) is the second largest genus, with 272 species, followed by *Pelargonium* (Geraniaceae), *Agathosma* (Rutaceae), *Phylica* (Rhamnaceae), *Lampranthus* (Aizoaceae), and *Oxalis* (Oxalidaceae), each with between 118 and 148 species (Table 3). Thirty-six genera have over 50 species and 13 genera have over 100 species. The 10 largest genera contribute over 21%, or 1935 species, to the flora. The next 10 largest genera contribute an additional 922 species. The 20 largest genera in the Cape flora thus contain over 31% of the total species.

There is no one unifying ecological pattern evident in the species-rich genera. *Agathosma, Aspalathus, Cliffortia, Erica, Phylica,* and the two largest genera of Proteaceae, *Leucadendron* and *Protea,* are best developed on sandy soils and are most

Table 4. Selected statistics for the CFR and various comparable regions (emended from Bond & Goldblatt, 1984). The figures represent the percentage of the total flora. The ten largest genera were determined by species number.

Region	Mean sp. number per genus	10 largest genera	Percentage of total flora		Annual species
			Monocots	Asteraceae	
Cape flora	9.1	21.4	24.5	11.5	6.7
Southern Africa (incl. Cape flora)	9.6	15.1	23.0	11.0	7.0
Cape Peninsula	4.2	17.5	34.6	11.5	9.6
Natal	3.9	17.0	27.1	11.4	ca. 6.5
Eastern North America	5.2	21.8	28.2	12.7	8.7
Europe	7.8	14.0	18.0	12.0	?
California Flora	5.3	15.2	19.2	13.6	27.4
Sonoran Desert	3.3	12.8	12.1	15.0	21.4
Texas	3.9	10.2	24.4	13.4	20.4
Hawaii	4.4	81.0	11.8	15.9	0.04
New Zealand	5.1	26.3	27.3	12.5	6.0

diverse in montane habitats. In contrast, species of *Lampranthus, Moraea, Pelargonium, Oxalis, Gladiolus,* and *Crassula* appear to occur with equal frequency on nutrient-poor, nutrient-intermediate, or comparatively rich soils and favor lowland habitats. *Lampranthus* and *Crassula* are succulents, and *Disa, Oxalis, Gladiolus,* and *Moraea* are seasonal geophytes, as are some species of *Pelargonium.* The remaining genera among the largest 20 comprise mostly shrubs or small trees. A few species of *Pelargonium, Senecio, Crassula,* and *Helichrysum* are annual species. *Thesium* species are hemiparasitic shrubs.

The most obvious shared factors in diversified genera in the Cape flora seem to be either a shrubby habit or seasonal geophytism. Over 17% of the total species in the flora are geophytes with bulbs, corms, tubers, or rhizomes. The number of species with underground perennating buds would be even higher if plants with woody caudexes were regarded as geophytes.

The ratio of species per genus, 9.1 (9.3% excluding ferns) in the Cape flora (Table 4), is particularly high compared to other floras and is one of the highest in the world (Fenner et al., 1997), although southern Africa as a whole, including the Cape Region, has a comparable ratio (9.6%, fide Goldblatt, 1997). A ratio of three dicots to one monocot species in the Flora is close to the average for floras across the world. Although the proportion of monocots does not seem unusual, the monocot families that are represented in the Cape flora are most distinctive. Some half of the species in the monocot families are geophytic and belong in the petaloid monocot families, notably Iridaceae, Orchidaceae, Hyacinthaceae, and Amaryllidaceae. The proportion of monocot to dicot species, matching that elsewhere in the world, is thus no more than coincidence.

PALEOENDEMIC GENERA

The endemic and near-endemic families of the Cape Region are all small and contribute relatively few genera and species to the flora, and they are best regarded as paleoendemics. With the exception of the rhizomatous perennial *Lanaria,* members of these families are all evergreen, sclerophyllous shrubs. They are often summer-flowering, usually have small flowers, and typically grow on sandstone-derived soils. We speculate that these plants are relicts of an ancient temperate southern African flora adapted to nutrient-poor soils.

Among non-endemic families, these paleoendemic genera are often members of the geologically oldest communities, tropical thicket and evergreen forest. Especially notable are *Platylophus,* a monotypic genus of Cunoniaceae and one of two continental African members of this family. The other, *Cunonia capensis,* is common in the Cape Region but extends into eastern southern Africa. Other monotypic genera such as *Heeria* and *Laurophyllus* (Anacardiaceae), *Hartogiella* and *Maurocenia* (Celastraceae), *Lachnostylis* (Euphorbiaceae), and *Smelophyllum* (Sapindaceae) also exemplify the paleoendemic component of the depauperate tree element of the flora and mostly have ranges restricted to the southern or eastern portion of the Cape Region (Goldblatt & Manning, 2000).

In non-forest habitats there are few paleoendemic genera or species apart from members of the endemic (and near-endemic) families of the Cape Region. These include the monotypic shrublets, *Empleuridium* (Celastraceae) and *Ixianthes* (Scro-

Table 5. Comparison of life forms in the California flora, central Chile, and the CFR. Figures are percentages of total species number; perennials below include geophytes and graminoids. Data for California and Chile are from Kalin Arroyo et al. (1994).

Region	Percentage of total flora			
	Trees	Shrubs	Perennials	Annuals
Cape Region	2.5	53.3	37.5	6.7
California	4.6	11.0	56.2	30.2
Central Chile	2.9	17.8	63.4	15.8

phulariaceae or Stilbaceae, Olmstead et al., 2001). The small tree, *Hyaenanche* (Euphorbiaceae or Picrodendraceae, Savolainen et al., 2000), also monotypic, and *Metrosideros angustifolia* (Myrtaceae), a member of an otherwise Australasian genus, show an odd pattern for the tree flora. Their ranges are restricted to the western half of the Cape Region where there are few tree species. *Metrosideros angustifolia,* the only African member of Myrtoideae: Metrosiderinae, seems as geographically isolated from its closest relatives as *Cunonia* and *Platylophus.* Like *Metrosideros, Bulbinella* is also a Cape–Australasian disjunct, but in this case the radiation within the genus has occurred largely in the Cape Region. The dwarf, tree-like monocot *Prionium* (Thurniaceae), of watercourses in nutrient-poor sandstone soils, is widespread in the Cape region but extends some distance to the east. The other member of the family is the Brazilian shield genus *Thurnia,* the pair thus exhibiting an unusual disjunction. The taxonomically isolated *Oldenburgia* (Asteraceae–Mutisieae), with three Cape species and one occurring a short distance beyond its eastern limits, is perhaps another example of that distribution pattern, for its closest allies occur in the Guyana Highlands. The small number of paleoendemic taxa emphasizes the huge contribution that recent speciation in a narrow range of families and genera has made to the total species diversity in the Cape Region.

LIFE FORMS

In contrast to other mediterranean floras, the Cape flora has relatively few trees, and this life form only accounts for some 220 species, about 2.5% of the flora. Trees in the California flora account for 4.6% of the species, but in Chile some 2.9% of the species are trees (Table 5). Most of the remaining elements of the Cape flora are shrubs and perennial herbs. The shrubby habit is the most common life form in the Cape Region, accounting for an estimated 4797 species, 53.3% of the total flora. Shrubs are diverse in form, but typically include species with sclerophyllous, and mostly microphyllous leaves, the characteristic that has given rise to the word fynbos, an Afrikaans word describing fine-leaved vegetation. Shrubs also include large numbers of species with succulent leaves (especially Aizoaceae). Stem-succulents include species of Apocynaceae and Euphorbiaceae, some of which are so reduced in size that the term shrublet hardly seems appropriate. The Cape flora stands out when compared to that of both California and Chile in the overwhelming proportion of shrubs (Table 5), which is largely explained by the nutrient-poor soils that favor this life form.

The Cape flora shows some notable differences with other mediterranean floras. One of these is a surprisingly low proportion of annuals—only some 609 species, about 6.7% of the total flora, as compared to 30% and 15% respectively for California and central Chile (Table 5) (Kalin Arroyo et al., 1994; Cowling et al., 1996). No comparable figures are available for the Mediterranean Basin. Although the proportion of annual taxa in the CFR is low, the annual flora is quite species rich. The total number of annual species is actually almost twice as high as the 378 annuals recorded in central Chile, an area of comparable size, and although the Cape has less than half the 1279 annuals in California, its area is only about one fourth that of California. For its geographic area then, the Cape flora is not depauperate in annuals, but its wealth of other life forms makes the annual habit appear under-represented. A small annual flora is also characteristic of southwestern Australia, an area that has a recent geological history comparable to that of the Cape Region and a similar pattern of nutrient-poor sandstone soils and richer clay. The low proportion of annuals in the Cape flora has remained without a satisfactory explanation since it was first noted by Bond and Goldblatt (1984) but the answer may simply lie in the disproportionate numbers of other life forms, especially microphyllous shrubs that are particularly well adapted to the nutrient-poor soils.

Two families, Scrophulariaceae and Asteraceae, are especially important in their contribution to the annual flora. Scrophulariaceae, with 166 species, contribute the largest number of annuals, and not, as might be expected, Asteraceae, which have some 138 annual species (Table 6). The Aizoaceae, Brassicaceae, Campanulaceae, Crassulaceae, Cyperaceae, Fabaceae, and Poaceae, each contribute between 20 and 35 species to the annual flora. Campanulaceae, in particular, need taxonomic

Table 6. Families with more than 10 annual species in the CFR. Total: 609 species (6.7% of the flora).

Family	Species number
Scrophulariaceae	166
Asteraceae	138
Campanulaceae	35
Brassicaceae	33
Poaceae	31
Aizoaceae	25
Fabaceae	25
Crassulaceae	23
Cyperaceae	21
Gentianaceae	18
Molluginaceae	16

Table 7. Total species (percentage in parentheses) of the different life forms in the Cape flora.

Life form	Species number	Species % of total flora
*Perennials	1025	(11.4)
Trees	221	(2.4)
Shrubs	4805	(53.2)
Geophytes	1575	(17.4)
Graminoids	795	(8.8)
Total, all perennials	8421	(93.3)
Annuals	609	(6.7)
Total	9030	(100)

* Perennials excluding trees, shrubs, geophytes, and graminoids.

study and our estimation of the number of species in the family, including its annual component, is subject to significant revision.

In contrast to the low proportion of annuals, the Cape Region has perhaps the highest proportion of geophytes of any part of the world, and is four to five times richer in this life form than is documented for other mediterranean floras (Esler, 1998; Esler et al., 1998; Goldblatt & Manning, 2000). At least 1550 species, over 17% of the total, have specialized underground organs including bulbs, corms, rhizomes, or tubers and are seasonally dormant (Table 7). The overwhelming number of geophytes are monocots, with over 1300 geophytic species, 662 of which belong to one family, Iridaceae. Most of these geophytes are seasonal and lie dormant underground in the dry season, but we have included in the geophyte category the few more or less evergreen species (e.g., *Agapanthus*, *Kniphofia*) with similar underground organs. The other main category of the monocots are the graminoids, that is, the perennial species of Cyperaceae, Juncaceae, Poaceae, Restionaceae, and a few other families, which account for 795 species (8.8% of the flora).

Vegetation

Far from having uniform vegetation, the Cape Region encompasses five biomes (Fig. 3) and several distinctive vegetation types, each with its own suites of species and physical characteristics (Rutherford & Westfall, 1994; Cowling & Holmes, 1992a). The most common and distinctive biome is heathland, locally called fynbos, an analogue of

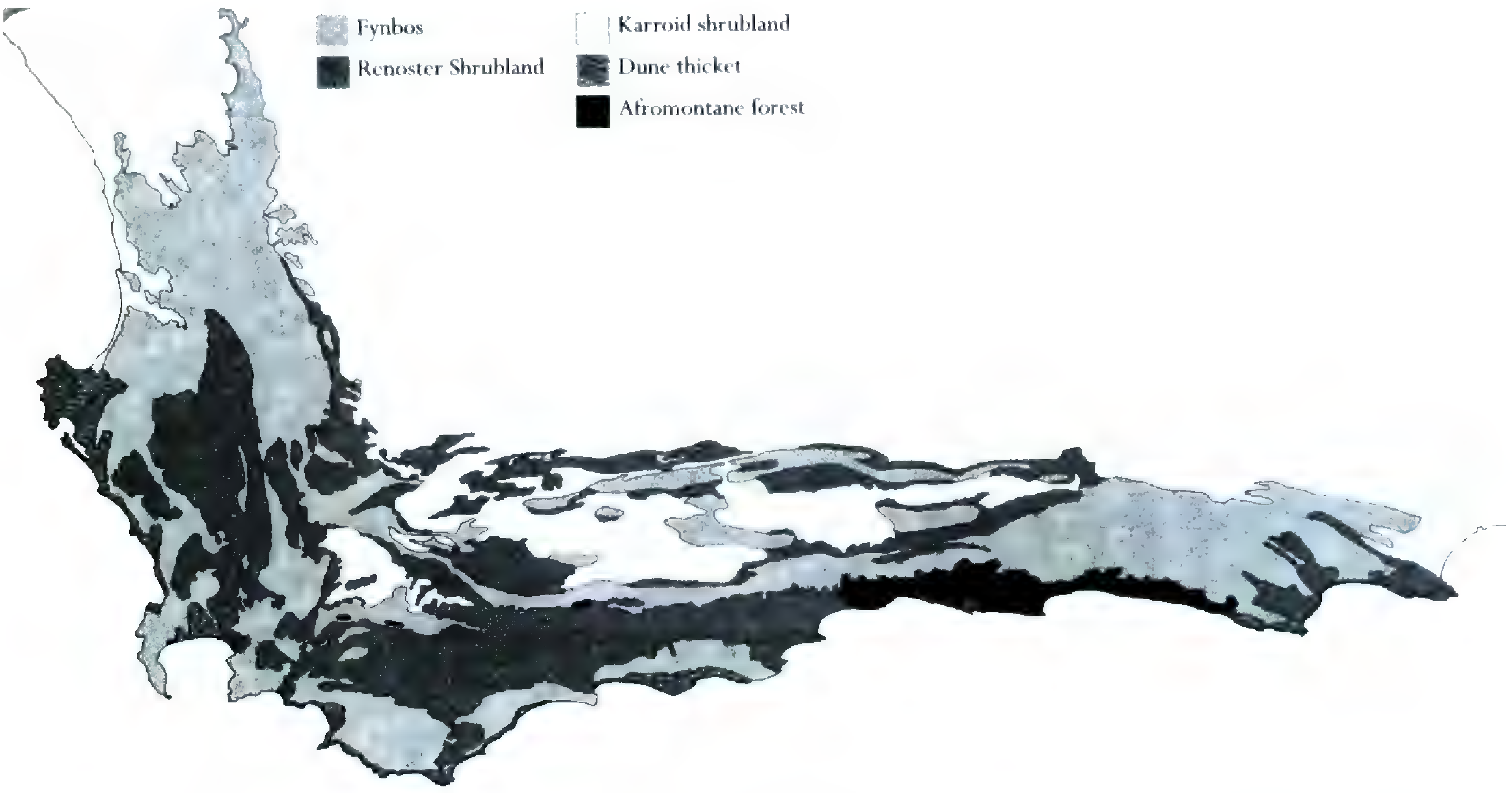

Figure 3. Major vegetation communities of the Cape Floristic Region (adapted from Louw & Rebelo, 1996).

Table 8. Comparison of species richness (indicated by species number per area), endemism, and the proportion of life forms in the floras of the six phytogeographic centers of the Cape flora (n/a = not available). For comparison, data are listed for the Cape Peninsula, a small area within the Southwest Center.

Floristic center (listed from west to east)	Physical area 10^3 km^2	Total species number	Species/ 10^3 km^2	% species endemic	Tree species	Annual species number (%)	Geophyte species number (%)
Northwest Center	22	4066	184.8	26.3%	69	415 (10.3)	855 (21.2)
Southwest Center	23	4661	202.7	32.0%	95	312 (6.8)	846 (18.2)
Agulhas Plain	3	1374	458.0	14.9%	24	92 (6.7)	202 (14.7)
Karoo Mountain	19	2151	113.2	15.5%	47	130 (6.1)	330 (15.5)
Langeberg Center	7	2363	337.6	11.7%	100	127 (5.4)	389 (16.4)
Southeast Center	18	2832	157.3	9.7%	163	156 (5.5)	427 (15.1)
Cape Peninsula	4.7	2250	478.7	7.5%	n/a	n/a	n/a
Cape Region	90	9030	100.3	68.7%	221	609 (6.7)	1575 (17.4)

Californian chaparral and Mediterranean maquis. Shrubs with ericoid or short, narrow, often needle-like leaves predominate, but most species of Proteaceae, a family common in this vegetation, have broad sclerophyllous leaves. Fynbos typically occurs on sandstone soils. A second distinctive vegetation type, renosterveld, is usually restricted to richer fine-grained soils. It shares few species with fynbos although they often grow adjacent to one another. Microphyllous Asteraceae are common in renosterveld, which consists of a dense shrubland with a rich herbaceous understory that becomes evident after fire or clearing but is often suppressed under a mature shrub cover. Dry sites with rainfall less than 200 mm p.a. support a vegetation of small succulent-leafed shrubs, including many Aizoaceae and Asteraceae, in a biome called succulent karoo. Thicket (a dense, semi-succulent and spinescent evergreen shrubland to low forest) and evergreen forest make up the remaining biomes.

Fire is an integral part of the ecology of the Cape Region and accounts for several aspects of the vegetation (Cowling, 1987). Growth form in mature fynbos and renosterveld is a relatively uniform, closed, low canopy of twiggy and microphyllous to sclerophyllous shrubs. These vegetation types are highly prone to periodic fire. Fire itself has a disruptive effect on the vegetation. It has obviously been a feature of the ecology for so long that there is a large flora of ephemerals, geophytes, other perennials, and short-lived shrubs that appear in the years following a fire, often flower profusely, and subsequently disappear, as they are succeeded by longer-lived shrubs. The long-term ecological consequence of fire on the flora is the existence of a niche for species that grow rapidly after fire to persist and bloom in the immediate post-fire years. This fire-adapted suite of species contributes substantially to the overall diversity in the flora. Mature vegetation is affected by fire in more subtle ways, but fire may cause local perturbations in species composition and the elimination of some taxa.

Diversity

Regional Diversity

The patterns of endemism within the Cape Region are fairly consistent, and examination of these patterns in selected genera that have diversified largely on sandstone substrates has resulted in the recognition of several regional centers of endemism (Fig. 1, Table 8). Weimarck (1941) pioneered this field, which has now been refined by Cowling and his coworkers (e.g., Cowling & Holmes, 1992a; Cowling & McDonald, 1999). The presence of these centers suggests that exchange between them is limited because of effective geographic isolation or because different microclimates in each center favor local species at the expense of migrants.

One aspect of our account of the Cape flora (Goldblatt & Manning, 2000) has been the formal recognition of phytogeographic centers so that distributional data for species can be analyzed within the CFR. Thus, we have been able to estimate for the first time the floristic diversity for each center. To some extent the statistics are approximate because some centers are under-collected (or under-cited in taxonomic accounts). We suspect that the Karoo Mountain Center (KM) and the Agulhas Plain Center (AP) have more species (and thus lower levels of endemism) than our data suggest (Fig. 1).

At the geographic center of the Cape Region, the Southwestern Center (SW) has the largest number of species (4661) and the highest level of endemism (32%). The Northwestern Center (NW) follows in taxonomic size (4066 species) and endemism (26.3%). The Karoo Mountain and Southeastern

Centers have much smaller floras and substantially lower levels of endemism. Much smaller in extent, the Langeberg (LB) and Agulhas Plain (AP) Centers understandably have smaller floras. The Southeastern Center (SE), of almost the same physical size as the NW and SW Centers, has a markedly smaller flora (2832 species), and only 9.7% endemism. This may be explained by its more equable and apparently less diverse climate or simply by higher levels of extinction during colder and drier periods of the Pleistocene. Differences in levels of endemism across the Centers are striking. The SW and NW Centers each have about twice the proportion of endemic species as the others, which may be a reflection of their greater climatic diversity.

The different life forms are unevenly distributed across the Cape Region (see Table 8), and the numbers of species of the two most distinctive life forms, annual species and geophytes, drop dramatically moving from west to east. The summer-dry NW and SW Centers have the largest numbers of geophytes and the highest proportion of geophyte species in the Cape flora, 21.2% and 18.2%, respectively. These two centers each have over 50% of all the geophytes in the entire CFR. In comparison, the other centers have between 14.7% and 16.4% geophytes. Annual species are more common in the west, and the NW Center has 10.3% annual species, while the remaining Centers each have no more than 6.8% annuals. The NW Center alone has 65% of the total annual species in the Cape flora. The distribution of trees shows the converse, with relatively few tree species in the NW Center and the highest numbers by far in the SE Center, which may be explained by its less pronounced seasonality and more predictable rainfall. Cowling (pers. comm.) suggests that proximity to the source pool of species for recolonization during warmer (e.g., Holocene) periods is probably the most important factor in explaining tree distributions.

These patterns seem directly related to climate. Both geophytes and annual species seem best adapted to a seasonally extreme climate with a wet winter and dry summer. A climate with higher, seasonally more evenly distributed rainfall, characteristic of the LB and SE Centers, seems likely to favor a tree flora and fewer geophytes and annuals. Like annuals, geophytes are adapted for survival in semi-arid, seasonal habitats. This is reflected in the greater representation of annuals and geophytes in the western half of the Cape Region, where summer precipitation is lowest. The unexpectedly high numbers of trees in the SW Center reflect the dissected landscape with the presence of fire-sheltered valleys and the regular occurrence of rainfall in the summer along its southern coast and interior.

COMPARISONS WITH OTHER FLORAS

An aspect of the Cape flora that is of particular interest is the high level of species diversity, both regional and local. For its size (ca. 90,000 km^2), the number of species of vascular plants in the CFR, 9030 (8918 seed plants plus 112 pteridophytes), is comparable with areas of the wet Neotropics (Table 9). Thus Panama (75,000 km^2) has 7300 seed plant species and Costa Rica (54,000 km^2) may have over 9000 species (see Table 9). In fact, southern Africa as a whole has a particularly rich and diverse flora for a predominantly temperate region. The area customarily treated for floristic purposes as southern Africa (Botswana, Lesotho, Namibia, South Africa, and Swaziland) has about 20,500 native vascular plant species in an area of 2,674,000 km^2, and South Africa alone may have some 18,500 species (ca. 18,275 seed plants plus 245 pteridophytes) in 1,221,000 km^2 (C. de Wet, pers. comm.). This is striking compared with an estimated 19,000 species in all of North America north of Mexico (19,341,000 km^2), or the estimated 16,500 native vascular plant species (15,800 seed plants plus ca. 700 pteridophytes) recognized for Peru, an area of 1,285,000 km^2 (Brako & Zarucchi, 1993; Zarucchi, pers. comm.). To put this in a regional context, all of tropical Africa may have about 26,500 species (Lebrun & Stork, 1997), in an area nearly 10 times larger than that of southern Africa and about 250 times as large as the Cape Region. Southern Africa and North Africa have approximately 21,500 additional species (those not shared with adjacent tropical Africa), making a total of ca. 47,000 species for the entire African continent. The tiny Cape Region, less than 0.5% of the total area of Africa, then has about one fifth of all the species on the continent. Subtropical southern Africa, excluding the Cape Region, has only about 14,300 species, a figure comparable with that for Tropical East Africa (Polhill, unpublished data). For the African continent then, not only is the Cape Region remarkably rich in species, but southern Africa has a higher species diversity than would normally be predicted given the general trend that species diversity increases toward the equator.

The species richness in the Cape flora is, by any measure, remarkable. Moreover, some 6208 or about 68.7% of the species are endemic there (Table 9). The high degree of species endemism in the Cape flora compared to the California Floristic Province, for example, with some 4240 species,

Table 9. Comparison of endemism of native vascular plants in selected regions of the world. References: 1. C. de Wet (pers. comm.); 2. Brako & Zarucchi (1993), Zarucchi (pers. comm.); 3. Raven & Axelrod (1978); 4. Kalin Arroyo et al. (1994); 5. Kalin Arroyo & Cavieres (1997); 6. Beard (1970); 7. Hopper (1992); 8. Hammel & Grayum (pers. comm.); 9. D'Arcy (1987); 10. Wagner (1991), Wagner et al. (1990); 11. Schatz et al. (1996); 12. Médail & Quézel (1997).

	Physical area 10^3 km^2	Number of genera	Genera endemic %	Total species	Species endemic %	Reference	Species/ 10^3 km^2
Continental areas							
Southern Africa	2674	2130	20.0	20,367	80.3	1	7.6
Peru	1285	2210	2.1	16,500	31.2	2	12.8
Areas of mediterranean climate							
Cape Region, South Africa	90	990	16.4	9030	68.7		100.3
California floristic province	324	806	6.5	4240	47.7	3	13.1
Central Chile 1	104	591	—	2395	ca. 22.5	4	23.0
2	155	—	—	2537	ca. 23.4	5	16.4
Southwestern Australia	270	462	ca. 20	3650	68	6	13.5
				or ca. 8000	ca. 75	7	29.6
Moist to wet tropics							
Costa Rica	54	1877	—	ca. 9000	—	8	166.7
Panama	75	1800	—	7300	ca. 15	9	97.3
Tropical or temperate islands							
Hawai'i	16.6	267	15	1138	86	10, 11	68.6
New Zealand	268	393	10	1996	81	3	7.4
Madagascar	594	ca. 1000	—	ca. 11,500	ca. 80	11	19.4
Mediterranean islands							
Crete	ca. 9	—	—	ca. 1706	ca. 10	12	189.6
Peloponnese	21	—	—	2400	ca. 12.5	12	114.3
Sardinia	24	—	—	2054	ca. 6	12	85.6
Sicily	26	—	—	ca. 2700	ca. 10	12	103.8

47.7% endemic (Raven & Axelrod, 1978), underscores the peculiarities of the Cape flora (Table 9). Such levels of endemism are usually associated with islands that have been isolated for long periods of geologic time, or with areas that have very sharp boundaries limiting direct plant migration. In a biological sense, the Cape Flora Region is virtually an island, not surrounded by ocean, but by a zone of dry climate or sharply different soils, or of seasonal rainfall distribution. The flora of southwestern Australia shares with the Cape Region an unusually high endemicity for a local continental flora (Beard, 1970; Hopper, 1992), and so does that of southern Africa as a whole (Table 9). Why the latter region should have such a high level of endemism is not at all clear.

The high level of diversity and local endemism of the CFR is starkly emphasized by comparison of the phytogeographic centers of the region with other areas. The SW and NW Centers each have over 4000 species and over 31% or 26% endemism, respectively, compared with about 2400 species and an estimated 22–23% endemism (depending on the geographical definition of the region) for the entire mediterranean flora of Chile (Table 9), an area over five times greater than either of these phytogeographic centers of the Cape flora. Likewise, important centers of local endemism (hot spots) within the Mediterranean Basin, including the islands of Sicily, Sardinia, and Crete, or the Peloponnese Peninsula, all of more or less comparable size to the NW or SW Centers, have approximately half or less than half the number of species and between 6% and 12.5% endemism (Médail & Quézel, 1997).

ALPHA DIVERSITY

Aspects of plant species diversity have been addressed on several levels, and it has been shown that at the local level selected areas within the Cape Region are not unusual on a world scale (Cowling et al., 1992; Goldblatt, 1997) and are less species-rich than many areas sampled in the New and Old World lowland tropics (Gentry, 1988a, 1988b). Patterns of alpha diversity (the number of species in a homogeneous community, e.g., Cowling et al., 1992) in a range of vegetation types in the Cape Region, including fynbos, renosterveld, forest thicket, and evergreen forest, are surprising. Fynbos sites (with seasonal species not included in species counts) have a mean alpha diversity of 68 species per 1000 m^2, with 121 the highest number of species recorded at any site (Cowling et al., 1992). Fynbos diversity is by no means uniform, and data indicate that diversity is higher in the west than the south and in sites of intermediate productivity than in either more mesic or drier sites (Bond, 1983).

Non-fynbos sites have been less well studied. Figures in the literature for renosterveld include means of 66 (Tilman et al., 1983) and 84 (Cowling et al., 1992) species per 1000 m^2. Forest thicket sites have a mean of 59 species per 1000 m^2, forest sites have ranges of 44 to 52 species, and succulent karoo shrublands a mean of 43 species in the same area (Tilman et al., 1983).

Comparisons made by Cowling et al. (1992) indicate that California chaparral communities have alpha diversity levels around 34 species per 1000 m^2 but the more comparable southwestern Australian region has an average of 69 species per 1000 m^2 in heathland (kwongan), a vegetation type similar to fynbos. While these figures are consistent with higher total species richness in the CFR and southwestern Australia compared with the California Floristic Province, they do not explain the comparable regional diversity of the CFR and the lowland wet tropics. In the wet tropics mean alpha diversity of trees (including woody lianas) alone has been found to range from 129 species (Africa) to 140 species (Neotropics), to 193 species (Asia) per 1000 m^2 (Gentry, 1988b), about twice the alpha diversity found in mediterranean communities on nutrient-poor soils. Inclusion of epiphytes and other herbaceous plants raises alpha diversity in tropical sites. Gentry and Dodson (1987) have shown that a major component of the plant species diversity in tropical forests actually lies with the epiphytes. Similarly the inclusion of seasonal geophytes would increase the figures for the Cape flora, and until more comprehensive surveys are made any comparisons can only be tentative.

BETA AND GAMMA DIVERSITY

Beta diversity (species turnover along a habitat or environmental gradient, Cowling et al., 1992) is relatively high in the Cape Region. Cowling (1990), for example, has reported nearly complete replacement in sites along the Agulhas plain that differed in soil features but were climatically and topographically similar. Differences in composition between communities on sandstone versus clay soils are so nearly complete that the plants on these two soils are treated as belonging to different vegetation types.

Gamma diversity (species turnover in equivalent habitats along geographic gradients, also called delta diversity, Cowling et al., 1992) is likewise extremely high in the Cape Region, and is reflected

in the high levels of regional endemism. Species replacement values of 46–70% have been reported by Kruger and Taylor (1979) for sites 25 km apart, and Linder (1985) has suggested that geographic replacement may account for 30% of the differences in species composition along geographic gradients in similar habitats. These figures are, however, lower than some estimates for lowland Neotropical sites (B. Boyle in Goldblatt, 1997).

Reasons for Cape Floristic Diversity

Richer in species than any other temperate flora and most tropical ones occupying comparable physical area (Table 9), the Cape flora is also highly distinctive. One of five regions in the world with a mediterranean climate, the Cape has substantially more species than do either California or central Chile, which are substantially larger in land area. Although southwestern Australia has a flora that may have about the same number of species as the Cape Region (Table 9), it is at least three times larger in area. Only the Mediterranean Basin, approximately 25 times larger in area, has a flora that is larger than the Cape flora, with about 2.5 times as many species. A formal comparison of these patterns is provided by Cowling et al. (1996). The reasons for the substantially higher species diversity of the Cape Region compared with these floras are several, and include a range of factors, both physical and historic.

A diversity of soils, a rugged landscape, and extremely variable and complex rainfall patterns have combined in the Cape Region to produce a mosaic of sharply different habitats that lie in close proximity to one another in a pattern repeated across its entire area. This high physical heterogeneity, although striking, is not unique to the region, and may even be greater in other regions. For example, the California Floristic Province has a wide range of soils, including serpentine substrates not present in the Cape Region, diverse climates, a rugged topography with higher mountains than those in the Cape, plus a wider latitudinal extension. Likewise, the Mediterranean Basin, orders of magnitude larger than the CFR, has a wide diversity of soils and a rugged landscape, with the mountains also higher than those found in the CFR. Both areas are often cited as being species-rich compared to neighboring regions, yet both are substantially poorer in species than the Cape Region, California in absolute number, and the Mediterranean area in substantially less alpha diversity per unit area. Southwestern Australia, in contrast, which has a flora approaching that of the Cape in size, noticeably lacks the rugged topography of other Mediterranean regions, although it exhibits some of the ecological features of the Cape Region. Physical heterogeneity alone cannot therefore account for the richness of the Cape flora, and edaphic factors as well as historical biogeography may be more significant.

Of the five mediterranean regions of the world only the Cape and southwestern Australia have soils that include large areas of nutrient-poor quartzitic sands, and at least part of the explanation for the higher species numbers here has been thought to relate directly to the particular effects of this substrate on plant life. High levels of local diversity have been considered characteristic of nutrient-poor soils (Tilman, 1982, 1983) and if this is correct, then the mere existence of large areas of such soils should account for the comparatively high alpha diversity of heathland vegetation in both South Africa and southwestern Australia compared with that in California or central Chile unless high levels of local and regional richness are not coupled. This hypothesis is, however, not supported either in the Cape or southwestern Australia, where alpha diversity levels on nutrient-poor and nutrient-intermediate soils appear to differ only minimally (Goldblatt, 1997). Although nutrient-poor soils may not support a flora significantly richer than that occurring on soils of other nutrient status in the Cape, they are able to maintain particularly high beta diversity in the associated fynbos vegetation, both on geographical gradients and on slightly different soils under the same climatic conditions. Comparable data for nutrient-intermediate and nutrient-rich sites are not yet available. Nutrient-poor soils in mediterranean climate zones have a higher proportion of reseeding versus resprouting shrubs (Wisheu et al., 2000), and these authors argue that this directly contributes to higher diversity because the high frequency of fires that destroy reseeders would lead to their shorter generation times and thus higher speciation rates. The high frequency of fire in areas of low-nutrient soils is thus another aspect that may contribute to diversity in the Cape Region. Fire is also significant in southwestern Australia and California but not in the mediterranean zone of Chile (Kalin Arroyo et al., 1994).

The combination of edaphic and topographic diversity, steep local climatic gradients, peculiar nutrient-poor soils, and frequent fires, although undoubtedly important in promoting species diversity in the Cape Region, is still inadequate to explain the presence of the unusually rich flora in the Cape Region, particularly when compared to southwestern Australia. A notable and perhaps crucial difference between the Cape and other areas of med-

iterranean climate, possibly excluding southwestern Australia, lies in their Pliocene–Pleistocene climatic history. Available data indicate a history for southern Africa very different from that experienced in the Northern Hemisphere and to a lesser extent Chile (Villagrán, 1994). Cycles of extreme cold and aridity alternating with warm wet phases made these areas largely uninhabitable by anything resembling their current floras, elements of which either became extinct or were locally restricted to sites of relatively mild climate. A similarly dynamic history for the Cape flora has been hypothesized in which Pleistocene glacial cycles caused a northward shift in the winter-rainfall zone, which in turn caused a northward expansion of the flora during the pluvial periods but local extinction and its restriction to refugia during dry periods (Axelrod & Raven, 1978). The limited evidence available for the Cape Region, however, indicates a more moderate climate without changes of such cataclysmic dimensions. Pollen cores reflect comparatively modest shifts in the flora (Meadows & Sugden, 1991), even in the semi-arid and ecologically sensitive Cedarberg mountains. Changes there might be expected to have been more severely influenced by the drier and colder climatic conditions that are postulated to have occurred during glacial periods, when belts of vegetation adapted to mediterranean climates contracted away from the dry zones that lay toward the equator. The absence of any evidence of major changes in the vegetation of the Cape Region during the Pleistocene suggests that the glacial cycles did not have the catastrophic effects on plant life in southern Africa that they did in the Northern Hemisphere or Chile. In the CFR relatively drier and wetter cycles may simply have induced changes in the local composition of vegetation, perhaps causing limited extinction, which in turn created opportunities for speciation.

The unusually high species richness of the Cape flora is thus, in all likelihood, a consequence of sustained climatic stability and reliability, enabling a more or less uninterrupted evolution and diversification of the flora to occur in a region of high physical complexity. The history of this evolution can be traced to some extent by considering the modes of speciation evident in the flora. Although there are few such studies for plant groups centered in the Cape flora, the available evidence suggests that parapatric speciation linked to substrate or microclimatic differences is an important mode of speciation in some families (Linder & Vlok, 1991; Cowling & Holmes, 1992b; Goldblatt & Manning, 1996). Vicariant species exhibit differences in ecology such as edaphic, microclimatic, seasonal, or pollination characteristics. For example, vicariant species of *Rhodocoma* (Restionaceae), a genus restricted to nutrient-poor sandstone soils in montane habitats, favor different habitats and are not significantly isolated geographically (Linder & Vlok, 1991). Parapatric speciation also appears to have been more important than geographic isolation in Agulhas Plain shrubs (Cowling & Holmes, 1992b) and in the genus *Lapeirousia* (Iridaceae) in the CFR and adjacent parts of the southern African west coast (Goldblatt & Manning, 1996). High levels of both beta and gamma diversity likewise support the hypothesis that microgeographic speciation has played a major role in speciation in the Cape flora. Nearly adjacent habitats with the same climatic and topographical conditions, which differ only in their substrates (coarse sand or fine sand or limestone), can support plant communities that differ radically in their species composition while still being broadly similar in family and generic composition (Cowling & Holmes, 1992a).

Parapatric or microgeographic speciation may actually be the rule not the exception in plants (Levin, 1993), and is favored by reduced gene flow across strong selection differentials. The mosaic of contrasting substrates that characterizes the CFR appears to provide such a strong selective differential. Although the Cape flora may not differ from other floras in mean pollen dispersability (Linder, 1985), many of its most characteristic elements have low seed dispersal distances. The majority of species in the Cape Region show no evident adaptations for seed dispersal and are regarded as passively dispersed, with estimated seed dispersal distances under 5 m (and most likely much less than this) (Linder, 1985). Dispersal in most Aizoaceae is by rain drops falling on hydrochastic capsules, and this mechanism, although an active one, results in very small dispersal distances (Desmet & Cowling, 1999). Active seed dispersal by ants is disproportionately well represented in both the Cape Region (Bond & Slingsby, 1983) and Australia (Berg, 1975). Some 1000 Cape species, notably in the families Fabaceae, Proteaceae, Restionaceae, Rhamnaceae, and Rutaceae, produce seeds with lipid bodies (elaiosomes) that are attractive to ants, and an undetermined additional number are transported to underground nests by harvester ants. In vegetation types prone to frequent fires, such as fynbos, the burial of seeds is a valuable adaptation (Cowling & Holmes, 1992b). However, dispersal distances for ant-dispersed seeds are also short, up to 6 m (Linder, 1985). More effective dispersal strategies are relatively restricted in their occurrence. Wind-dispersal is characteristic of many As-

teraceae and Orchidaceae (which have comparatively low levels of endemism in the Cape flora), while long-distance dispersal involving flying vertebrates (birds and bats) is least common, and is especially rare in plants on nutrient-poor substrates. There is an assumption that plants on such soils cannot afford to allocate resources to protein-rich berry or drupaceous fruits (Bond & Slingsby, 1983). The low frequency of fruits with burs and spines, adapted for exochory, suggests that dispersal by non-flying vertebrates has long been unimportant in the flora, perhaps because the fauna has historically been a small one in terms of numbers of species and individuals. This may be due largely to the unpalatability, low nutrient status, and low productivity of the flora as a whole.

Indirect evidence of the importance of reduced gene flow distances in stimulating local species diversity comes from a comparison of the number of species and their level of endemism between taxa with widely dispersed seeds and those with reduced dispersal distances. Genera with fleshy diaspores or those that are well adapted for wind dispersal tend to have wide ranges, few species per genus, and low levels of local endemism. Compare the berry-fruited *Nylandtia* (Polygalaceae), which has two species, with its relative *Muraltia*, which has dry fruits and over 100 species, most with narrow ranges. Similarly, *Chasmanthe* (Iridaceae), which has fleshy or deceptive (brightly colored) seeds, has two widespread species and one localized one, whereas its close relative *Tritonia*, which has dry seeds, has 16 species in the flora, most of them with narrow ranges. Another striking example is *Chrysanthemoides* (Asteraceae), which has seeds enclosed in a fleshy pericarp. The two species of the genus extend throughout the Cape Region and one far beyond it into tropical Africa. The numerous species of the closely related genera *Osteospermum* and *Tripteris* have dry seeds and mostly have smaller geographic ranges. This comparison is also instructive at the family level. Low seed dispersability is typical of many of the larger and most characteristic families in the flora with high ratios of species to genus and high levels of local endemism. Ericaceae, Iridaceae, and Fabaceae, which largely lack highly developed mechanisms for long-distance seed dispersal, have ratios of above 20 species per genus and higher than 80% endemism at the species level. Levels of local and regional endemism for Asteraceae (63% endemic species) and Orchidaceae (60.8%), mostly with wind-dispersed seeds, and Poaceae (38.6%) and Anacardiaceae (32.1%), many with fruits adapted to wind and/or animal dispersal, show levels of local and regional endemism below the mean for the entire flora (68.7%).

The massive speciation in the Cape flora is, we suggest, most likely explained by a model of local speciation in the absence of catastrophic climatic or topographic perturbations. It appears that a relatively stable climate prevailed in the Cape during the Pleistocene and that local parapatric speciation across steep environmental gradients may account for a considerable proportion of the speciation events that occurred in the CFR. Because of this relative stability it seems reasonable to postulate that extinction rates in the main vegetation zones, fynbos, renosterveld, and succulent shrubland, were low and more than compensated for by local speciation events. The nutrient-poor soils scattered in a mosaic across the CFR must have stimulated local speciation rates because of the characteristic low vagility of the seeds in the great majority of the plants adapted to these soils. Likewise, the low vagility of many of the species in Succulent Karoo, although likely a result of different selective forces, has the same consequences, with high levels of local speciation, and thus high levels of diversity across geographic, environmental, and edaphic gradients (e.g., Cowling & Holmes, 1992b; Cowling et al., 1998; Desmet & Cowling, 1999).

The unusually high diversity of the Cape flora is matched by its extraordinary composition of families and genera. Instead of a balanced flora with relatively small numbers of species per genus there has been massive local radiation in a series of unrelated genera. This is so pronounced that almost 22% of the total species in the Cape Region fall in just 10 genera, while the 20 largest genera account for over 30% of the total species (Table 3). Typical examples of these genera are *Erica* (over 650 spp.), *Aspalathus* (272 spp.), *Agathosma* (143 spp.), *Phylica* (133 spp.), and *Cliffortia* (114 spp.). Significantly, none of the genera that display a pattern of massive local radiation in the Cape Region are endemic there, but rather they extend northward into Namaqualand, eastward into southern KwaZulu-Natal, or even further to the northeast into tropical Africa. They are, however, primarily restricted to nutrient-poor soils wherever they occur.

In sharp contrast to these examples are the endemic families of the Cape flora, which are without exception depauperate in species, although they may contain several genera. These families are typically restricted to montane habitats in acidic sandstone soils, and many of their constituent species are highly local endemic plants of particular mountain chains or peaks. They display the characteristics of paleoendemism and probably represent el-

ements of a previously more widespread southern temperate flora adapted to nutrient-poor soils in a summer-rainfall regime. It is probably no coincidence that most of these species flower in summer, and are thus out of phase with the spring flowering peak of the flora. With the development of a winter-rainfall climate in the Pliocene (e.g., Coetzee, 1993), it is reasonable to infer that these pre-Cape flora elements were gradually restricted to mesic sites in which some moisture was present over the summer months. Concomitantly it appears that other elements of the flora were able to radiate into emerging niches, thereby establishing the huge neo-endemic element of the flora. The highly sclerophyllous or microphyllous habit developed by taxa adapted to nutrient-poor substrates can thus be regarded as an important pre-adaptation to the mediterranean climate. The highly seasonal nature of the mediterranean climate, as well as its regularity, would also have favored families and genera with a geophytic habit, for example, Amaryllidaceae, Hyacinthaceae, Iridaceae, and Oxalidaceae.

The rapid and extensive radiation of plant taxa in the CFR must have been favored by both the emergence of new habitats through climatic change and the exposure of the coastal plain as sea levels fell at times during the Pleistocene (Coetzee, 1993), as well as by the stability of the climate. At the same time the flora was increasingly isolated by the winter wet and summer dry climate regime from recruitment from the summer-rainfall-adapted flora of adjacent parts of southern Africa, which largely lack the low- or nutrient-intermediate soils so characteristic of the Region.

A final characteristic of the Cape flora is the great, and often extreme, diversity of flower form that is a feature of many of the genera. This is linked to a diversity of pollination strategies, many of which are poorly exploited outside the region. In particular, pollination by sunbirds, long-proboscid flies, hopliine beetles, rodents, and the butterfly *Aeropetes* are more extensively developed in the Cape flora than elsewhere in Africa (Manning & Goldblatt, 1996; Goldblatt et al., 1998; Goldblatt & Manning, 1999). All these strategies favor differently shaped, large, brightly colored flowers. Pollinator diversity is likely to be part of the explanation for the high species diversity in the CFR, particularly for certain families in the flora. Both Iridaceae and Ericaceae, for example, have adopted a range of pollination strategies not evident or only weakly expressed elsewhere across their range (Vogel, 1954; Goldblatt & Manning, 1996, 1998; Bernhardt & Goldblatt, 2000), and are often particularly striking when in bloom. In *Gladiolus*, a prime example of a genus with diverse pollination systems and represented in the CFR by 106 species, the genus exhibits no less than 27 shifts in pollination system in southern Africa, most of these in the CFR (Goldblatt et al., 2001), and repeatedly evolved adaptations for long-proboscid fly, sunbird, moth, and butterfly pollination, which must have played a major role in its radiation. The short season favorable for both plant and insect growth is probably the overriding factor responsible for the diversification of pollination strategies and, more than anything else, has made the Cape flora so extremely appealing to human sensibilities.

Conservation

Like other parts of the world with species-rich floras and an expanding human population, there are varied and serious threats to the Cape flora. Expanding agricultural activity for growing food or to supply other human needs has transformed lowland areas near population centers to the extent that little or no native plants remain locally (Rebelo, 1992). Moreover, the peculiarly local distribution of many Cape plants (high beta diversity) means that a higher proportion is imminently threatened with extinction than would be the case with widespread species. The number of species known to be lost forever is relatively low, but the number of species represented by single, reduced, and diminishing populations is alarmingly high. Taylor (1978) estimated that some 500 endemic species in the CFR were threatened, while at least 60 species were known to be extinct (0.67%). Red Data Book numbers for southern Africa in 1985 include 1320 Cape plants (14.67% of the total) (Hall & Veldhuis, 1985). Criteria for classification of threatened species vary; Rebelo (1992) estimated 218 threatened species (extinct, endangered, or vulnerable) in the CFR (ca. 4.8%), slightly less than half the figure provided by Taylor, but nevertheless, considerable.

In 2001 these figures are certain to be higher as a result of the expanding human population, despite ever more sophisticated conservation activity. A peculiar threat to the Cape flora is the spread of alien vegetation, largely woody species of Australian *Acacia* and *Hakea* and European *Pinus*. These species rapidly invade montane and lowland areas not currently suitable for agriculture, thus compounding the threats of agricultural activity and urban growth. The threat posed by this alien vegetation is being vigorously countered by biological control methods and manual removal, but the problem is immense and requires constant monitoring. Kruger (1977) estimated that 60% of fynbos had

been replaced by alien vegetation, agriculture, or urban development. Twenty-five years later, this figure is bound to have increased.

Concrete examples may better illustrate the situation. Rebelo (1992) estimated that of 306 endemic species of Proteaceae 65 were threatened (defined as extinct, endangered, or vulnerable) (ca. 21%), while 131 were treated as Red Data species. The pattern in other families is similar, although slightly less serious, with 10.5% of endemic Iridaceae, 9% of endemic Rutaceae, ca. 3% of endemic Ericaceae, ca. 2% each of endemic Asteraceae and Fabaceae threatened (Rebelo, 1992). The number of species of each of these families included in the Red Data Book is substantially higher (Hall & Veldhuis, 1985).

A detailed analysis of reserves and other conservation areas in the CFR is presented by Rebelo (1992). Recent conservation efforts have secured substantial areas for preservation of diverse vegetation types in the CFR and a framework for a conservation plan to establish reserves to cover portions of all vegetation types has been developed (Cowling & Heijnis, 2001; Cowling et al., 2001). Although such reserves cannot include populations of all endangered species because of their erratic distributions, future loss of distinctive vegetation types will be limited and preservation of substantial tracts of each will in the future be enhanced.

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Statistical Summary of Some of the Activities in the Missouri Botanical Garden Herbarium, 2001

	Vascular	Bryophyte	Total
Acquisition of Specimens			
Staff Collections	31,270	7,494	38,764
Purchase	201,004	35,000	236,004
Exchange	23,088	1,812	24,900
Gifts	7,837	1,705	9,542
Total acquisitions	263,199	46,011	309,210
Mountings			
Newly mounted at MO	70,177	23,093	93,270
Specimens mounted when acquired	14,004	0	14,004
Repairs			
Specimens repaired	13,482	n/a	13,482
Specimens stamped	1,566	n/a	1,566
Total repairs	15,048	0	15,048
Specimens sent			
On exchange	22,102	160	22,262
As gifts	19,242	628	19,870
Total	41,344	788	42,132
Loans sent			
Total transactions	359	38	397
Total specimens	22,749	2,879	25,628
To U.S. institutions			
Transactions	192	23	215
Specimens	13,028	1,948	14,976
To foreign institutions			
Transactions	167	15	182
Specimens	9,721	931	10,652
To student investigators			
Transactions	50	13	63
Specimens	6,772	1,207	7,979
To professional investigators			
Transactions	309	25	334
Specimens	16,161	1,672	17,833
Loans Received			
Transactions	233	28	261
Specimens	23,980	2,882	26,862

	From U.S.A.	From abroad	Total
Visitors	234	92	326

During 2001, 108,840 specimens were accessioned into the herbarium: 93,270 mounted at MO, 14,004 mounted when acquired, and 1566 old MO specimens stamped (and numbered). The total number of mounted, accessioned specimens in the herbarium on 1 January 2002 was 5,219,216 (4,832,175 vascular plants and 387,041 bryophytes).

Purchases in 2001 included approximately 187,000 vascular plants and 35,000 bryophytes in the Clyde F. Reed Herbarium (see Missouri Bot. Gard. Bull. 89(6): 16. 2001). The estimated 162,000 mounted vascular plants should be repaired as needed, stamped, and accessioned in the near future. The unmounted vascular plants will be mounted, the bryophytes packeted, and all accessioned as resources allow. In addition, the bryophyte collection from LAF, approximately 30,000 specimens, accumulated and curated by William Dean Reese (1924–2002), was acquired on permanent loan in late 2001.

The Garden's herbarium is closely associated with its database management system, TROPICOS (see ⟨www.mobot.org/mobot/research⟩). The charts below summarize some of the statistics from TROPICOS both for the calendar year 2001 and as year-end totals. Note that the specimen records in TROPICOS are primarily based on MO specimens, meaning that about thirty-seven percent of the bryophytes (an increase of about six percent over 2000) and thirty-two percent of the vascular plants (an increase of about one percent) in the herbarium are now computerized, with an overall total of about thirty-two percent (an increase of about one percent).

TROPICOS records—Calendar Year 2001 Additions

	Bryophytes	Vascular Plants	Total
Specimens	30,709	94,277	124,986
Names	931	25,453	26,384
Synonyms	872	12,097	12,969
Distributions	369	31,376	31,745
Types	152	19,040	19,192
Bibliography	1,170	3,605	4,775

TROPICOS records—Year-End 2001 Totals

	Bryophytes	Vascular Plants	Total
Specimens	143,298	1,548,109	1,691,407
Names	100,431	795,401	895,832
Synonyms	63,415	392,242	455,657
Distributions	39,028	798,765	837,793
Types	7,583	278,617	286,200
Bibliography	23,274	64,654	87,928
Specimens in herbarium	387,041	4,832,175	5,219,216
Percent of specimens computerized	37	32	32

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—Marshall R. Crosby

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PHYLOGENETIC RELATIONSHIPS OF THE GENUS *PIPTOCHAETIUM* (POACEAE, POOIDEAE, STIPEAE): EVIDENCE FROM MORPHOLOGICAL DATA[1]

Ana María Cialdella[2] *and Liliana Mónica Giussani*[2]

Abstract

A systematic treatment of the entire genus *Piptochaetium*, which complements that of Cialdella and Arriaga for the South American species, is presented herein. A synopsis of 36 species and 2 varieties, a key to identify these species, as well as synonymy and geographical distribution, are given. Illustrations and photographs of diagnostic characters are presented for the North American species for the first time. We propose a phylogenetic hypothesis for the genus based on morphological and anatomical characters. Monophyly of *Piptochaetium* was supported by the combination of three synapomorphies: a grooved palea, involute lemma margins that fit into a longitudinal palea groove, and the palea protruding from the lemma. Two sections were previously recognized in *Piptochaetium*: *Podopogon* and *Piptochaetium*. The cladistic analysis showed that only South American species of *Piptochaetium* sect. *Piptochaetium*, together with *P. brevicalyx*, form a monophyletic group (Obovoid group), while *Piptochaetium* sect. *Podopogon* is polyphyletic. Therefore, the taxonomic recognition of sectional taxa cannot be supported. Phylogenetic relationships of two varieties of *Piptochaetium stipoides* (var. *stipoides* and var. *echinulatum*) were not clearly resolved. Furthermore, based on cladistic analyses, taxonomic observations, and the study of type material, *Piptochaetium tovarii* subsp. *pilosa* is raised to specific rank (= *P. pilosum*).

Key words: phylogenetic relationships, *Piptochaetium*, Poaceae, Stipeae.

Resumen

Se presenta un tratamiento sistemático de todo el género *Piptochaetium*, que complementa el propuesto por Cialdella y Arriaga para las especies sudamericanas. En este trabajo, se presenta una sinopsis de las 36 especies y 2 variedades, una clave para identificar las especies, su sinonimia, distribución geográfica y observaciones. Se incluyen por primera vez ilustraciones y fotografías de los caracteres diagnósticos para las especies norteamericanas. Se propone una hipótesis

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filogenética basada en caracteres morfológicos y anatómicos. Mediante el análisis filogenético, fue confirmada la monofilia de *Piptochaetium* sobre la base de tres sinapomorfías: una pálea surcada entre los nervios, los márgenes de la lemma involutos insertos en el surco longitudinal de la pálea y la pálea asomando por entre los márgenes de la lemma. Dos secciones fueron previamente reconocidas para *Piptochaetium*: *Podopogon* y *Piptochaetium*. Como resultado del análisis cladístico, sólo las especies sudamericanas de la sección *Piptochaetium*, junto con *P. brevicalyx*, conformaron un grupo monofilético (grupo Obovoide). Consecuentemente, en este tratamiento, no se considera válido el reconocimiento de categorías formales infragenéricas. En el análisis, se incluyeron 2 variedades de *Piptochaetium stipoides* (var. *stipoides* y var. *echinulatum*) y la posición filogenética de ambas variedades no fue claramente resuelta. *Piptochaetium tovarii* subsp. *pilosa* fue elevada al rango de especie (= *P. pilosum*), sobre la base del estudio filogenético, las observaciones taxonómicas y el estudio del material tipo.

Piptochaetium J. Presl is an American genus distributed mainly in temperate areas of both hemispheres and scarcely represented in tropical regions of the Andes (Parodi, 1944; Barkworth, 1986; Sánchez Vega, 1991; Cialdella & Arriaga, 1998). The genus belongs to the tribe Stipeae and was established by Presl in 1830, based on *Piptochaetium setifolium* J. Presl [= *P. panicoides* (Lam.) E. Desv.]. It includes perennial, caespitose plants, generally less than 1.5 m tall, with loosely or densely flowered panicles of one-flowered spikelets; membranous glumes, frequently longer than the floret, enclose the anthecium. Three characters are useful for recognizing the genus: the grooved palea, involute lemma margins that fit into a longitudinal palea groove, and the palea protruding from the lemma.

The South American species of *Piptochaetium* have been studied by Parodi (1944), who treated 21 species in 2 sections: *Piptochaetium* sect. *Podopogon* (Raf.) Parodi and *Piptochaetium* sect. *Piptochaetium* (= *Piptochaetium* sect. *Eupiptochaetium* Parodi). Sánchez Vega (1991) treated the 6 species for Peru, and grouped them into the sections proposed by Parodi. Cialdella and Arriaga (1998) published a more recent treatment of the South American species, in which they recognized 27 species, 2 subspecies, and 2 varieties for both sections, considering leaf anatomy and micromorphological characters of the lemma in their analysis. The North American taxa were studied by Valencia and Costas (1968) with emphasis on cytological characters, and they recognized 7 species. A comparison of these treatments, including the infrageneric classification, is shown in Table 1. In a revision of the North American Stipeae, Barkworth (1986) treated 13 species in North and Mesoamericas without grouping them into sections.

The aim of this work is to complete the morphological account of the genus by considering the species not included in the previous paper by Cialdella and Arriaga (1998). This study comprises a synopsis of 36 species and 2 varieties, a key to identify them, and their associated synonymy and geographical distribution. A phylogenetic analysis of *Piptochaetium* was performed to explore the relationship among species, using cladistic methodologies with the morphological data.

Materials and Methods

Morphological Study

This study was based on the analysis of almost 1000 herbarium specimens, including type material for most of the analyzed taxa (Appendixes 1, 2). The specimens studied were from BA, BAA, BAB, BAL, C, CAS, CEN, CORD, CPUN, CTES, G, ICN, K, LE, LP, LPB, MO, MEXU, MVM, MVFA, NY, P, PR, SGO, SI, SRFA, UNR, US, USM, UTC and XAL (Holmgren et al., 1990).

Micromorphological structures of the lemma were analyzed using a scanning microscope Zeiss DSM 940 A, located in the Instituto de Botánica Darwinion and as summarized in Cialdella and Arriaga (1998: 108). Epidermal appendages (macrohairs, prickles, hooks, and papillae) follow the classification proposed by Ellis (1979).

Cladistic Analysis

Twenty-nine exomorphological and epidermal characters were used in the cladistic analysis (Appendix 3); all multistate characters were treated as unordered. Only two autapomorphies were included in the analyses: characters 20 and 27 (Cialdella & Arriaga, 1998: figs. 3D and 9F, respectively). Characters were directly observed from herbarium material totaling nearly 1000 specimens. The data matrix is presented in Table 2.

Two different computational strategies, using minimum parsimony, were used to analyze phylogenetic relationships among species of *Piptochaetium*. In both cases, polymorphic characters were included (Table 2). One strategy assigned all characters equal weight. This analysis was performed using NONA version 1.6 (Goloboff, 1993a). In the second strategy, a concavity function of the homoplasy (K = 3) was

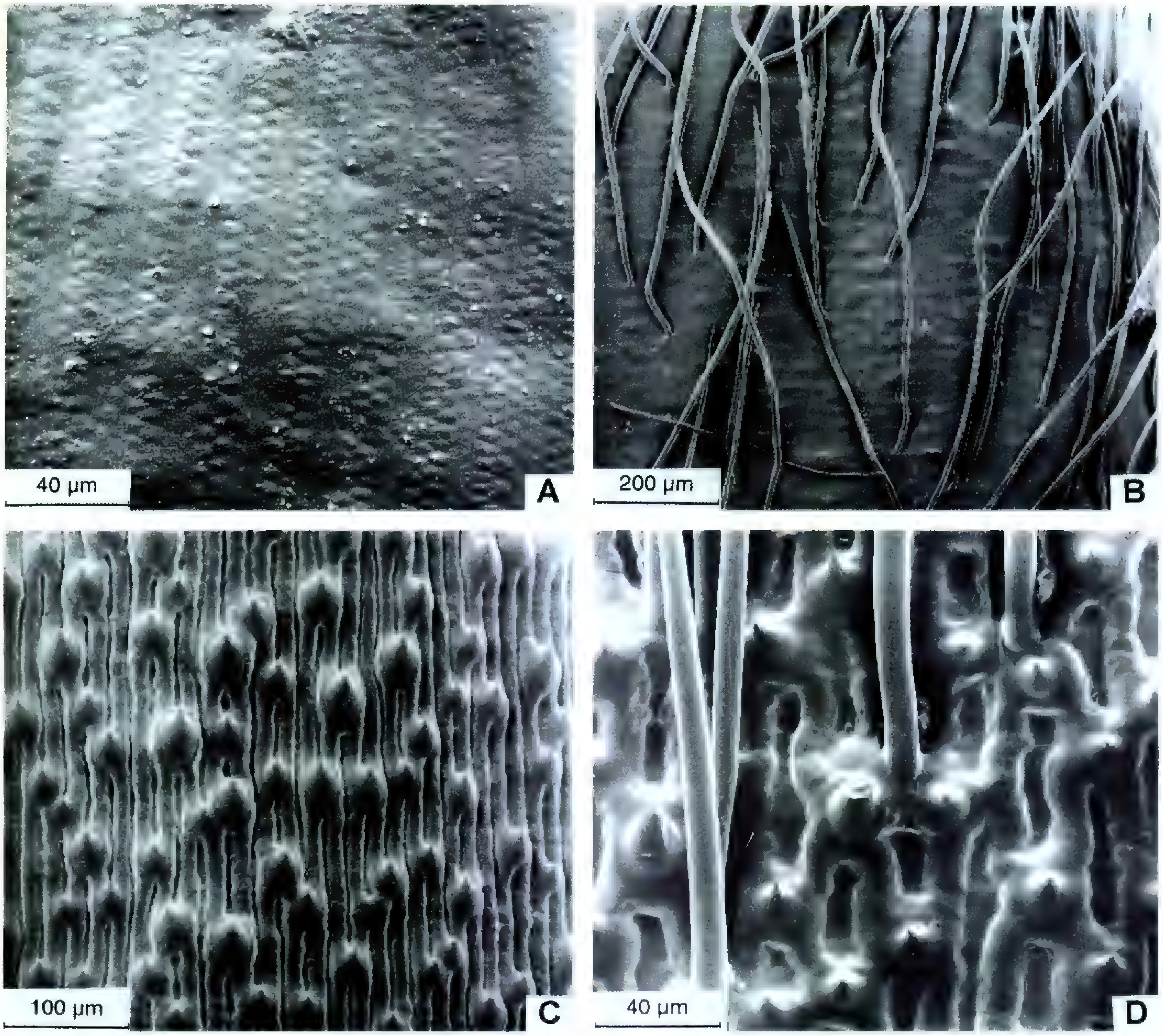

Figure 1. SEM photos showing epidermal characters of the lemma of *Piptochaetium*. —A. Lemma without any epidermal appendages of *P. brevicalyx* (*Rzedowski 35863*). —B. Macrohairs of *P. fimbriatum* (*Davidse et al. 29775*). —C. Prickles and hooks of *P. arenaceum* (*Harvey 1854*). —D. Prickles, hooks, and macrohairs of *P. angustifolium* (*Palmer 726*).

used to apply weight to all characters, a method for estimating implied weight (Goloboff, 1993b). This analysis required Pee-Wee version 2.8 (Goloboff, 1997). In both analyses, settings amb- (clades resolved only if they have unambiguous support), and poly = (polytomies allowed) were used to resolve phylogenies. The order of taxa was randomized, creating a Wagner tree and submitting it to branch-swapping by means of tree-bisection reconnection (TBR) using the sswap* command. To evaluate the relative support of clades, branch support, with instruction "bsupport" (bs) of NONA (Bremer, 1988, 1994), was calculated.

INGROUP

Since Desvaux (1853), *Piptochaetium* has been recognized by the presence of a grooved palea, and this character was diagnostic to distinguish the genus from its allies (Spegazzini, as *Oryzopsis* Michx. sensu Speg., 1901; Parodi, 1944; Barkworth, 1990; Peñailillo, 1996; Cialdella & Arriaga, 1998). Other characters were also used to uniquely identify *Piptochaetium*, such as a palea longer than the lemma, protruding from the lemma apex, and the lemma margins involute and fitted into the palea groove. The 37 entities recognized within the whole genus were considered as terminal taxa.

OUTGROUPS

Nassella E. Desv. and *Hesperostipa* (Elias) Barkworth were selected as outgroups, based on their similarities in morphological and anatomical characters to *Piptochaetium* (Thomasson, 1978b; Barkworth, 1990) as well as previous phylogenetic relationships proposed by Barkworth (1990).

A detailed history of *Nassella* can be found in

Table 1. Infrageneric classifications within *Piptochaetium* in comparison with results from the phylogenetic analysis. Geographic distribution of the species is also presented. Abbreviations correspond to: Ar, Argentina; Bo, Bolivia; Br, Brazil; Ch, Chile; Co, Colombia; Ec, Ecuador; Gu, Guatemala, Me, Mexico; Pa, Paraguay; Pe, Peru; Ur, Uruguay; US, United States; Ve, Venezuela.

Sections sensu Parodi (1944)	Valencia & Costas (1968)	Sanchez Vega (1991)	Cialdella & Arriaga (1998)	Informal groups from the phylogenetic analysis	Geographical distribution
PODOPOGON	PODOPOGON	PODOPOGON	PODOPOGON	Polyphyletic group	
			P. alpinum	*P. alpinum*	Br
P. angustifolium ?				*P. angustifolium*	Me
P. avenaceum	*P. avenaceum*			*P. avenaceum*	Me, US
P. avenacioides ?	*P. avenacioides*			*P. avenacioides*	US
P. bicolor			*P. bicolor*	*P. bicolor*	Ar, Ch, Ur
P. brachyspermum			*P. brachyspermum*	*P. brachyspermum*	Ar
P. cabrerae			*P. cabrerae*	*P. cabrerae*	Ar
P. confusum			*P. confusum*	*P. confusum*	Ar, Ur
		P. featherstonei	*P. featherstonei*	*P. featherstonei*	Pe
				P. fimbriatum	Gu, Me, US
P. hackelii			*P. hackelii*	*P. hackelii*	Ar, Ur
P. indutum		*P. indutum*	*P. indutum*	*P. indutum*	Ar, Bo, Ec, Pe
= *P. bicolor*			*P. medium*	*P. medium*	Ar, Br, Ur
P. napostaense			*P. napostaense*	*P. napostaense*	Ar
			P. palustre	*P. palustre*	Br
				P. pringlei	Me, US
P. ruprechtianum			*P. ruprechtianum*	*P. ruprechtianum*	Ar, Br, Ur
		P. sagasteguii	*P. sagasteguii*	*P. sagasteguii*	Pe
				P. seleri	Gu, Me
P. virescens	*P. virescens*			*P. virescens*	Gu, Me, Ve
PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	PIPTOCHAETIUM	Obovoid Group	
	P. angustifolium				Me
P. angolense			*P. angolense*	*P. angolense*	Ch
P. brevicalyx	*P. brevicalyx*			*P. brevicalyx*	Me
P. burkartianum			*P. burkartianum*	*P. burkartianum*	Ar
P. calvescens			*P. calvescens*	*P. calvescens*	Ar, Ur
			P. cucullatum	*P. cucullatum*	Ur
P. fimbriatum	*P. fimbriatum*				Gu, Me, US
P. hirtum			*P. hirtum*	*P. hirtum*	Ar, Ch
P. jubatum			*P. jubatum*	*P. jubatum*	Ur

Table 1. Continued.

Sections sensu Parodi (1941)	Valencia & Costas (1968)	Sanchez Vega (1991)	Cialdella & Arriaga (1998)	Informal groups from the phylogenetic analysis	Geographical distribution
P. lasianthum			*P. lasianthum*	*P. lasianthum*	Ar, Br, Ur
P. lejopodum			*P. lejopodum*	*P. lejopodum*	Ar, Ur
P. montevidense		*P. montevidense*	*P. montevidense*	*P. montevidense*	Ar, Bo, Br, Ch, Ec, Me, Pa, Pe, Ve, Ur
P. panicoides		*P. panicoides*	*P. panicoides*	*P. panicoides*	Ar, Bo, Br, Ch, Co, Ec, Pe, Ve, Ur
		= *P. tovari* subsp. *pilosa*	= *P. tovari* subsp. *pilosa*	*P. pilosum*	Pe
P. pringlei	*P. pringlei*				Me, US
P. setosum			*P. setosum*	*P. setosum*	Ch, US
P. stipoides var. *echinulatum*	*P. stipoides* var. *echinulatum*		*P. stipoides* var. *echinulatum*	*P. stipoides* var. *echinulatum*	Ar, Ur
P. stipoides var. *stipoides*	*P. stipoides* var. *stipoides*		*P. stipoides* var. *stipoides*	*P. stipoides* var. *stipoides*	Ar, Br, Ch, Me, US, Ur
		= *P. tovari* subsp. *tovarii*	= *P. tovari* subsp. *tovarii*	*P. tovarii*	Ec, Pe
P. uruguense			*P. uruguense*	*P. uruguense*	Ar, Br, Me, Pa, Ur

Barkworth (1990). She expanded *Nassella*, including a total of 79 species, the majority of which were previously considered in *Stipa* L. The circumscription proposed by Barkworth (1990) was later accepted by Peñailillo (1996) and Torres (1997). In this sense, *Nassella* includes species with obovoid or terete florets, a short and blunt to long and sharp callus, strongly overlapping lemma margins, a lemma apex fused in a crown, and a highly reduced, nerveless and glabrous palea. All species considered in *Nassella* have a characteristic lemma epidermal pattern: short fundamental cells, with irregularly sinuate sidewalls and abundant short cells.

Hesperostipa was one of the nine sections of *Stipa* formally proposed by Elias (1942). Thomasson (1978a) noticed a very different epidermal pattern within this section in comparison with any other *Stipa*: long fundamental cells with strongly sinuous sidewalls, and absence of short cells. After studying North American Stipeae, Barkworth (1993) raised *Stipa* sect. *Hesperostipa* to the generic rank, in which she included four species: *Hesperostipa comata* (Trin. & Rupr.) Barkworth, *H. curtiseta* (Hitchc.) Barkworth, *H. neomexicana* (Thurber) Barkworth, and *H. spartea* (Trin.) Barkworth. *Hesperostipa* is endemic to North America and includes plants with narrowly terete florets, a sharp callus, and a persistent, twice-geniculate awn. The lemma is indurate, with flat margins, slightly or not overlapping; the palea is subequal to the lemma, prow tipped and 2-nerved (Barkworth, 1993).

Key to *Piptochaetium*, *Nassella*, and *Hesperostipa*

1. Palea longitudinally grooved, 2-nerved, longer than the lemma, and protruding from the lemma apex; lemma margins involute, fitting into the palea groove .... *Piptochaetium*

1′. Palea flat, 2-nerved or nerveless, shorter than or equal to the lemma, usually not protruding beyond the lemma apex; lemma margins flat 2

2(1). Lemma margins strongly overlapping; palea nerveless, less than one-third the length of the lemma .... *Nassella*

2′. Lemma margins not or slightly overlapping; palea 2-nerved, always as long as the lemma, apex prow tipped or "pinched" .... *Hesperostipa*

Results

Seven equally parsimonious trees were obtained when the characters were weighted equally. These were 58 steps long, with a Consistency Index (CI) = 0.55 and Retention Index (RI) = 0.87. When the analysis was performed without autapomorphies (characters 20 and 27), the CI was 0.53. When the characters were weighted, five equally parsimonious

Table 2. Data matrix used in the cladistic analyses for *Piptochaetium*. Numbers in the first row represent the characters described in the text, together with their codification. Numbers within brackets represent a polymorphism for the particular character of the species involved.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Nassella	0	0	2	0	0	0	[0 1]	[0 1]	[0 1]	[0 1]	[0 1]	0	[0 2 3]	[0 1]	[0 1]
Hesperostipa	0	0	0	1	1	2	1	0	1	0	[0 1]	0	0	0	[0 1]
Piptochaetium alpinum	1	1	1	1	1	1	1	0	1	0	1	1	0	0	1
P. angolense	1	1	1	1	1	1	0	1	1	1	0	0	2	1	0
P. angustifolium	1	1	1	1	1	1	0	0	1	0	1	0	0	0	1
P. avenaceum	1	1	1	1	1	1	1	0	1	0	[0 1]	0	0	0	0
P. avenacioides	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. bicolor	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brachyspermum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. brevicalyx	1	1	1	1	1	1	0	1	0	1	0	1	2	0	0
P. burkartianum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. cabrerae	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0
P. calvescens	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. confusum	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. cucullatum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. featherstonei	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. fimbriatum	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. hackelii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. hirtum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. indutum	1	1	1	1	1	1	1	0	1	0	0	0	0	0	1
P. jubatum	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. lasianthum	1	1	1	1	1	1	0	1	1	1	1	0	2	0	1
P. lejopodum	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. medium	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. montevidense	1	1	1	1	1	1	0	1	0	1	[0 1]	0	3	1	0
P. napostaense	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. palustre	1	1	1	1	1	1	1	0	1	0	1	0	0	0	0
P. panicoides	1	1	1	1	1	1	0	1	0	1	0	0	3	1	0
P. pilosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	1
P. pringlei	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. ruprechtianum	1	1	1	1	1	1	1	0	1	0	1	0	1	0	0
P. sagasteguii	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1
P. seleri	1	1	1	1	1	1	0	1	1	0	1	0	0	0	1
P. setosum	1	1	1	1	1	1	0	1	1	1	0	0	2	0	0
P. stipoides var. *echinulatum*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. stipoides var. *stipoides*	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. tovarii	1	1	1	1	1	1	0	1	0	1	0	0	2	0	0
P. uruguense	1	1	1	1	1	1	0	1	1	1	[0 1]	0	2	0	0
P. virescens	1	1	1	1	1	1	1	0	1	0	1	0	0	0	1

trees were obtained. These trees were also 58 steps long, their fit was 190.7, and the rescaled fit was 0.68. Although the trees obtained with the two strategies differed in some respects, both yielded the same strict consensus tree as well as the unambiguous synapomorphies that support clades (Fig. 3). Only the relationships within one clade, which involved *P. calvescens*, *P. cucullatum*, *P. jubatum*, *P. lejopodum*, *P. stipoides* var. *stipoides*, and *P. stipoides* var. *echinulatum*, differed between the strategies. Relationships among these species are not resolved on the consensus tree (Fig. 3). Figure 4 shows one of the seven hypotheses found with NONA. This tree is the most similar to one of the five trees found with Pee-Wee. They differ in the position of *P. alpinum* which, in Pee-Wee's results, is sister to the clade that includes *P. pringlei* to *P. palustre*; and they also differ in the order of *P. uruguense* and *P. angolense*, which are inverted in Pee-Wee analysis.

Cladistic analysis supports *Piptochaetium* as a monophyletic genus [Bremer support (bs) = 3]. It is clearly defined by three synapomorphies (Fig. 3): lemma margins involute (1), a boat-shaped palea (2), and a palea longer than the lemma (3; Fig. 2A, B).

Table 2. Extended.

	16	17	18	19	20	21	22	23	24	25	26	27	28	29
Nassella	[0 1]	[0 1]	[0 1]	0	0	[0 1]	[0 1]	0	[0 1]	0	[0 1]	0	[0 1]	0
Hesperostipa	0	1	1	0	0	0	1	0	1	0	1	0	0	0
Piptochaetium alpinum	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. angolense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. angustifolium	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. avenaceum	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. avenacioides	0	1	[0 1]	[0 1]	0	1	1	0	1	0	1	0	0	0
P. bicolor	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. brachyspermum	0	1	0	1	0	1	1	1	0	0	1	0	0	0
P. brevicalyx	0	0	0	0	0	1	1	0	0	0	0	0	1	0
P. burkartianum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. cabrerae	0	1	1	0	0	1	1	1	0	0	1	0	0	0
P. calvescens	[0 1]	1	1	0	0	1	0	1	0	1	1	0	1	1
P. confusum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. cucullatum	0	1	0	1	0	1	1	1	0	0	1	1	1	0
P. featherstonei	0	1	1	0	0	1	1	0	1	0	1	0	0	0
P. fimbriatum	0	0	0	0	0	1	1	0	[0 1]	0	[0 1]	0	1	0
P. hackelii	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. hirtum	0	0	0	0	0	1	1	0	0	0	1	0	1	0
P. indutum	0	1	1	0	0	0	1	0	0	0	1	0	0	0
P. jubatum	0	1	0	1	0	1	[0 1]	1	1	0	1	0	1	1
P. lasianthum	0	1	1	0	0	1	1	0	1	0	1	0	1	0
P. lejopodum	0	1	0	1	0	1	0	1	0	0	1	0	1	1
P. medium	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. montevidense	1	0	0	0	0	1	1	0	0	1	1	0	1	0
P. napostaense	0	1	0	1	0	0	1	0	1	0	1	0	0	0
P. palustre	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. panicoides	[0 1]	0	0	0	0	1	1	0	0	1	1	0	1	0
P. pilosum	0	1	1	0	0	0	1	0	0	0	1	0	1	0
P. pringlei	0	0	0	0	0	1	1	0	1	0	1	0	0	0
P. ruprechtianum	0	1	0	1	0	1	1	0	1	0	1	0	0	0
P. sagasteguii	0	1	1	0	0	0	1	0	1	0	1	0	0	0
P. seleri	0	1	1	0	0	1	1	0	1	0	1	0	[0 1]	0
P. setosum	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. stipoides var. *echinulatum*	0	1	1	0	1	1	0	1	0	1	1	0	1	1
P. stipoides var. *stipoides*	0	[0 1]	[0 1]	[0 1]	0	1	[0 1]	1	[0 1]	[0 1]	[0 1]	0	1	[0 1]
P. tovarii	0	0	0	0	0	0	1	0	0	0	0	0	1	0
P. uruguense	0	1	1	0	0	1	1	0	0	0	1	0	1	0
P. virescens	0	1	1	0	0	0	1	0	1	0	1	0	0	0

Hesperostipa is the most closely related group to *Piptochaetium*, as they share a 2-nerved palea (4) and long fundamental cells of the lemma epidermis (5).

South American species of *Piptochaetium* sect. *Piptochaetium*, together with *P. brevicalyx* from Mexico, are gathered in a monophyletic clade (bs = 2), which is now recognized herein as the Obovoid group (Fig. 3). It is supported by two synapomorphies: a deciduous awn (10) and obovoid florets (13, Fig. 5H). Three species are closely related to the Obovoid clade: *P. fimbriatum* (Fig. 5G), *P. seleri* (Fig. 5F), and *P. angustifolium* (Fig. 5E). *Piptochaetium fimbriatum* and *P. seleri* present a blunt or truncate callus (8; bs = 1) and, together with *P. angustifolium*, they all have a short callus (7; bs = 1). These three species are not included in the Obovoid clade, as they do not have a deciduous awn as well as a well-defined obovoid floret. They are North American species; *P. fimbriatum* and *P. seleri* were also found in Guatemala, with intermediate forms observed between the Obovoid clade and the rest of the species (Figs. 3 and 4; see discussion). Species of the Obovoid clade present the relation between length and width of the floret always less than 3.5

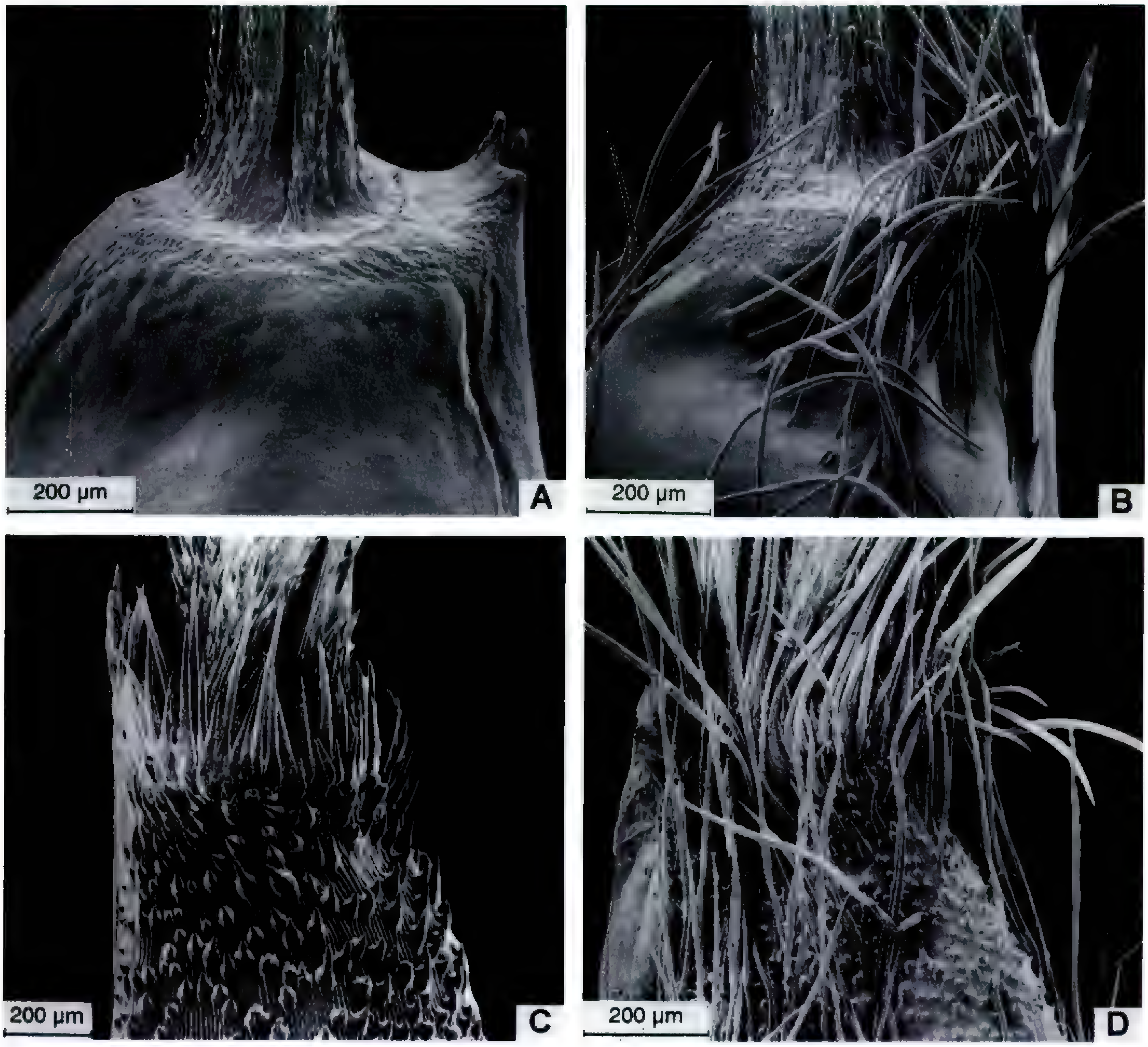

Figure 2. SEM photos showing distal portion of the floret with different crowns in *Piptochaetium*.—A. *P. brevicalyx* (*Rzedowski 35863*). —B. *P. fimbriatum* (*Davidse et al. 29775*). —C. *P. avenaceum* (*Harvey 1854*). —D. *P. angustifolium* (*Palmer 726*).

(28). However, this character is ambiguous for the clade that gathers the Obovoid group with *P. seleri* and *P. fimbriatum*, and consequently, this synapomorphy is not shown in Figure 3. An additional analysis was performed to test the influence of the intermediate species (*P. fimbriatum*, *P. angustifolium*, and *P. seleri*) on the results. Without these three species, the major clades and relationships among the species did not change.

All species of the Obovoid clade, except *P. lasianthum*, have densely flowered inflorescences (11), although for some species of this clade this character is variable. These species also have a crown without macrohairs (24), which reverts in *P. jubatum* and is polymorphic in *P. stipoides* var. *stipoides*. Species from *P. uruguense* to *P. stipoides* var. *echinulatum* form a clade defined by a glabrous lemma (15, Fig. 1A, 5H; bs = 1), and *P. pilosum* (= *P. tovarii* var. *pilosa* Sánchez Vega) is consequently apart from its counterpart *P. tovarii* (= *P. tovarii* var. *tovarii*), suggesting this rank is not appropriate. Species with a few prickles on the lemma (18) are gathered in a clade that includes species from *P. burkartianum* to *P. stipoides* var. *echinulatum* (bs = 1). This grouping is divided into two major clades. The first clade, *P. burkartianum*, *P. montevidense*, *P. panicoides*, *P. hirtum*, *P. brevicalyx*, and *P. tovarii* (bs = 1), is characterized by a lemma without prickles (17, Fig. 1A), and, except for *P. burkartianum*, the other species also have a glabrous callus (9; bs = 1). *Piptochaetium brevicalyx* and *P. tovarii* are related by the absence of prickles in the crown (26; bs = 1), while *P. montevidense* and *P. panicoides* are gathered in a clade (bs = 3) and share three synapomorphies: lens-shaped (13) and laterally compressed florets (14), and presence of papillae in the crown (25).

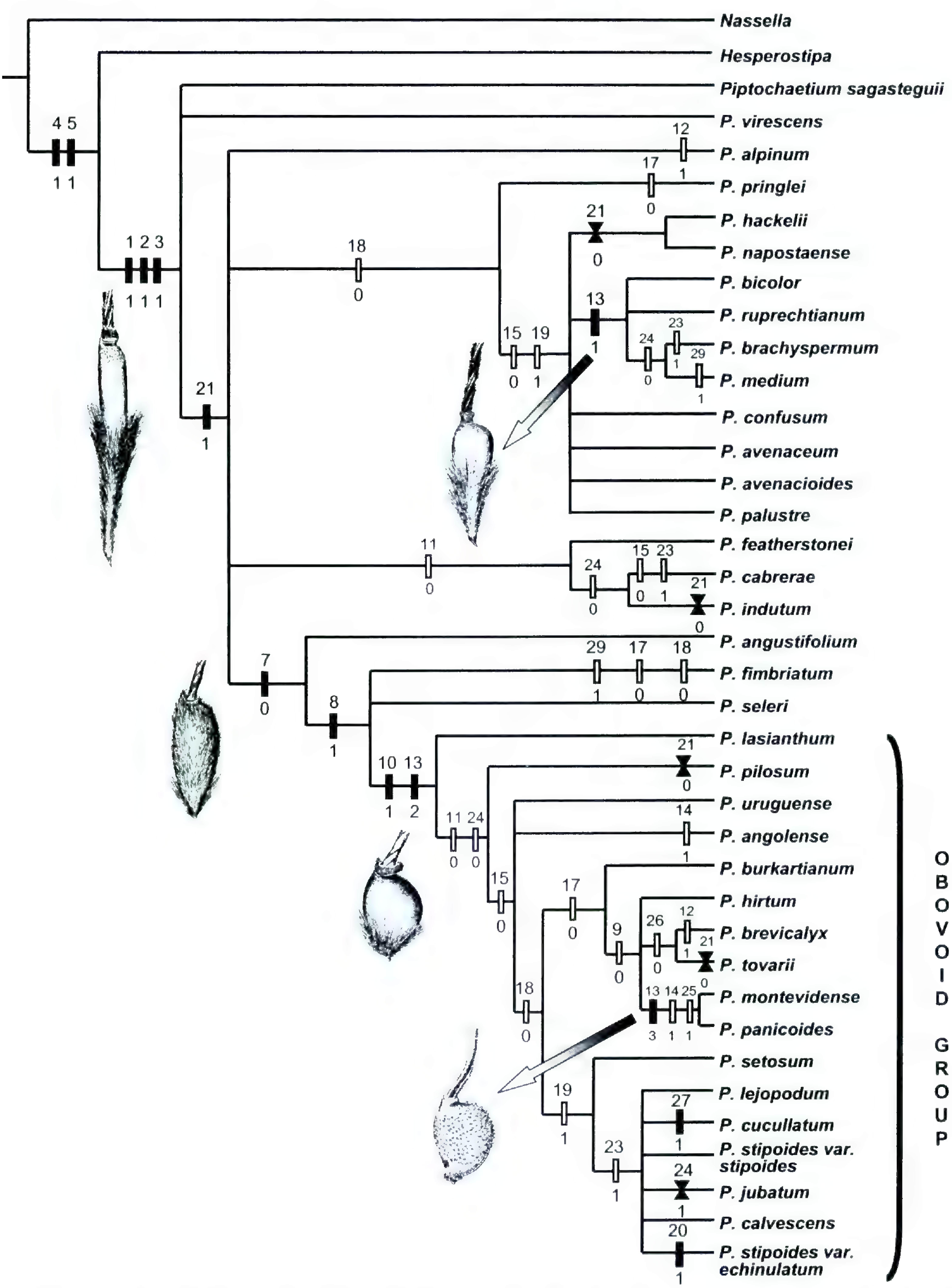

Figure 3. Strict consensus of seven equally parsimonious trees resulting from phylogenetic analysis of *Piptochaetium* (NONA program). A similar tree resulted from the strict consensus of five equally parsimonious trees under implied weight (Pee-wee program). Optimization of characters are shown on the tree: solid bars = unambiguous synapomorphies, empty bars = homoplastic character transformations, solid crosses = reversals. Character numbers (see Appendix 3) are above symbols, and character state changes are below bar or crosses. Illustrations show evolution of floret shape in *Piptochaetium* (see discussion).

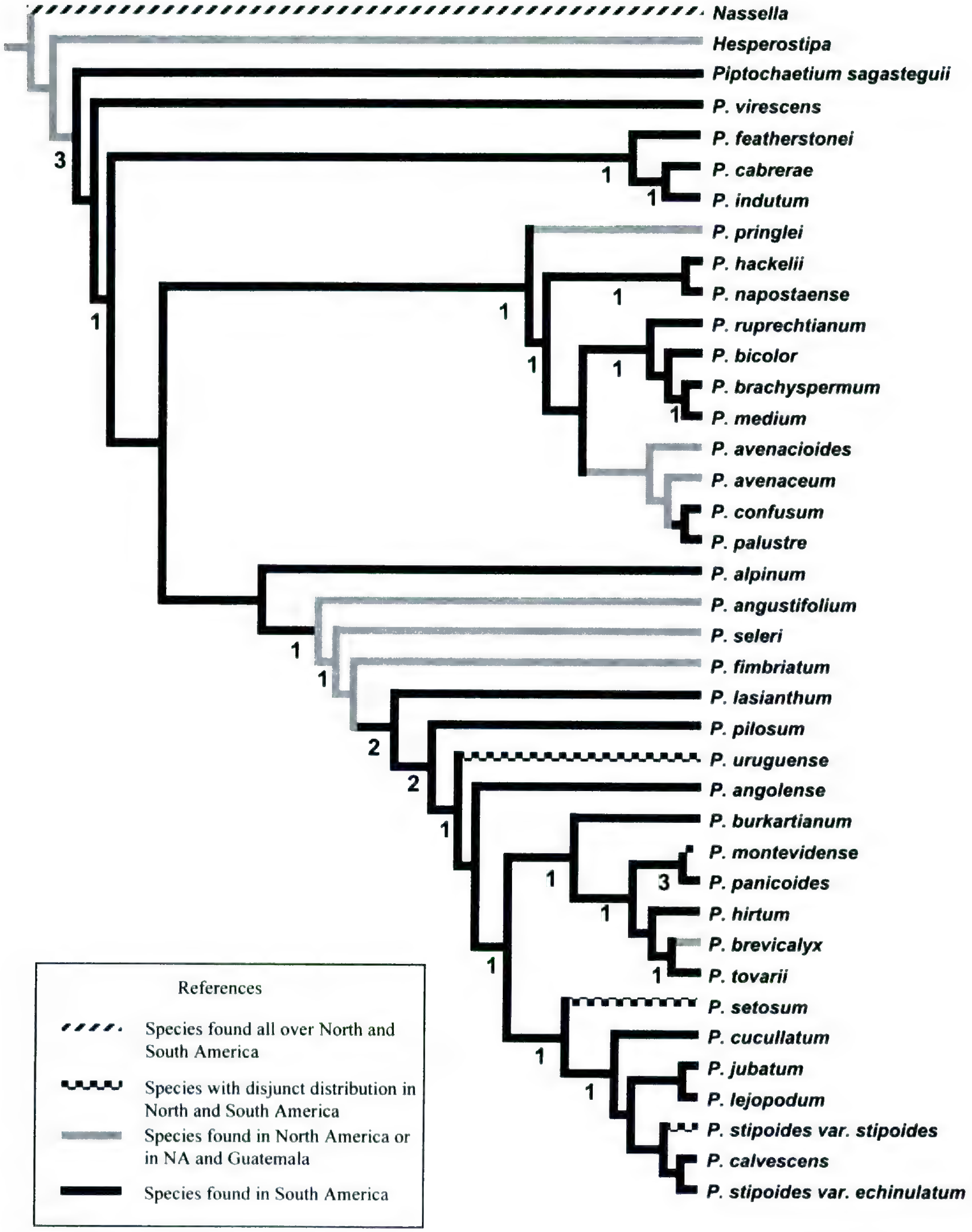

Figure 4. One of the seven equally parsimonious trees of 58 steps resulting from the phylogenetic analysis of *Piptochaetium* (NONA program), based on morphological and epidermal characters. Distribution of species is mapped on the tree as shown in the references. Numbers below branches represent the Bremer support value for each clade.

Lateral compression of the floret (14) is a derived character that occurs also in *P. angolense* (Cialdella & Arriaga, 1998: fig. 9C). The second major clade comprises *P. setosum*, *P. calvescens*, *P. cucullatum*, *P. jubatum*, *P. lejopodum*, and two varieties of *P. stipoides* (bs = 1). This clade is characterized by the presence of prickles in only one-third of the lemma (19), except *P. stipoides* var. *echinulatum*, which has prickles on almost all the lemma surface. With the exception of *P. setosum*, all other species have a rev-

olute crown toward the outside (23; bs = 1); and optimization of characters 9, 18, 19, 22, 25, and 29 is ambiguous on this clade. Relationships among species are not resolved within this clade. Only *P. brachyspermum* and *P. cabrerae* also have a revolute crown, a character that appears independently in these taxa.

Species traditionally included in *Piptochaetium* sect. *Podopogon* (Cialdella & Arriaga, 1998) resulted in a polyphyletic group. Species of this section are linked to some North American species, not included in any previous infrageneric classification (Table 1, Fig. 3). Some species of this section are gathered in stable clades based on unambiguous synapomorphies: *P. featherstonei*, *P. cabrerae*, and *P. indutum* have loosely flowered inflorescence branches (11; bs = 1), while *P. cabrerae* and *P. indutum* do not have macrohairs in the crown (24; bs = 1). *Piptochaetium cabrerae* is characterized by a glabrous lemma (15) and a revolute crown (23). A clade including *P. pringlei* (Fig. 5D) to *P. palustre* is distinguished by the absence of prickles over almost the entire lemma surface (18; bs = 1). All species of this clade (bs = 1), except *P. pringlei*, have a glabrous lemma (15), with prickles restricted to the distal third (19). *Piptochaetium hackelii* and *P. napostaense* are identified by a lemma as wide as the crown (21; bs = 1). This character appears as reversals in *P. indutum*, *P. pilosum*, and *P. tovarii*. Four species, *P. bicolor*, *P. brachyspermum*, *P. medium*, and *P. ruprechtianum*, are gathered in a clade (bs = 1) supported by the shape of the floret; all of them have obconical florets (13), rather than a terete to fusiform floret. *Piptochaetium brachyspermum* and *P. medium* are distinguished by the absence of macrohairs in the crown (24; bs = 1). Only *P. medium* has a wide floret with respect to its length (28, Cialdella & Arriaga, 1998: fig. 8B).

Only *P. cucullatum* (Cialdella & Arriaga, 1998: fig. 9F) presents a cone-shaped awn (27), and *P. stipoides* var. *echinulatum* (Cialdella & Arriaga, 1998: figs. 3D, 10J) has prickles with their bases covered by adjacent epidermal cells (20). *Piptochaetium brevicalyx* and *P. alpinum* present the upper glume as long as the lemma (12), although this character has an independent origin in both taxa.

Discussion

Piptochaetium is a monophyletic genus clearly defined by reproductive characters related with lemma and palea structures (Fig. 3). The origin of *Piptochaetium* was supposed to be in North America according to Thomasson (1978a, 1980), who related this genus with *Berriochloa* Elias as its ancestor. This fossil grass was first characterized by Elias in 1932. Thomasson (1978a, b, 1985) found some similarities between *Piptochaetium* and *Berriochloa* based on floret shape, which can be cylindrical, obovoid, obconical, or lens-shaped in both genera. Although he emphasized similarities between epidermal patterns of the lemma, *Berriochloa*, *Piptochaetium*, and *Hesperostipa* (treated as *Stipa* sect. *Hesperostipa* by Thomasson) share a similar lemma epidermis with long fundamental cells with sinuous sidewalls (Thomasson, 1978a, b, 1982). This study shows *Hesperostipa* to be more closely related to *Piptochaetium* than *Nassella*. A more comprehensive evaluation of the relationship of *Piptochaetium* to other genera in the tribe requires a more inclusive study.

Within *Piptochaetium*, species were grouped in two sections: *Podopogon* and *Piptochaetium* (Table 1) according to the revision carried out by Parodi (1944) and as later accepted by Valencia and Costas (1968), Sánchez Vega (1991), and Cialdella and Arriaga (1998).

As suggested by cladistic analysis, *Piptochaetium* sect. *Podopogon* is not a natural entity. Consequently, infrageneric ranks cannot be supported. The species traditionally included in *Piptochaetium* sect. *Piptochaetium* (Parodi, 1944), with the exception of *P. fimbriatum* and *P. pringlei*, were assembled in a monophyletic group, here informally called the Obovoid group, also including *P. brevicalyx*. This clade is supported by two synapomorphies: a deciduous awn and obovoid florets. The Obovoid clade shares other synapomorphies with three North American species: a short callus with *P. angustifolium* and a short and blunt callus with *P. fimbriatum* and *P. seleri*. Short and blunt calluses are derived states within the genus, while acute and long calluses are plesiomorphic states (Fig. 3). This agrees with Thomasson (1985), who found that all species of *Berriochloa*, regardless of the floret shape, always had an acute callus. He suggested that the evolution of the blunt callus in *Piptochaetium* is a post-Miocene event.

Transition in floret shape was observed by Thomasson (1978b) in fossils of *Berriochloa* in Nebraska. He found a change in the floret shape from the oldest to the youngest stratigraphic levels: cylindrical or cylindrical-fusiform shapes were found in the oldest levels, while the youngest levels presented all possible forms within the genus: cylindrical, cylindrical-fusiform, obovoid, as well as spheroid florets. The present study supports Thomasson's findings, showing that obconical, obovoid, and lens-shaped florets are always derived states (Fig. 3). Species with obconical florets form a

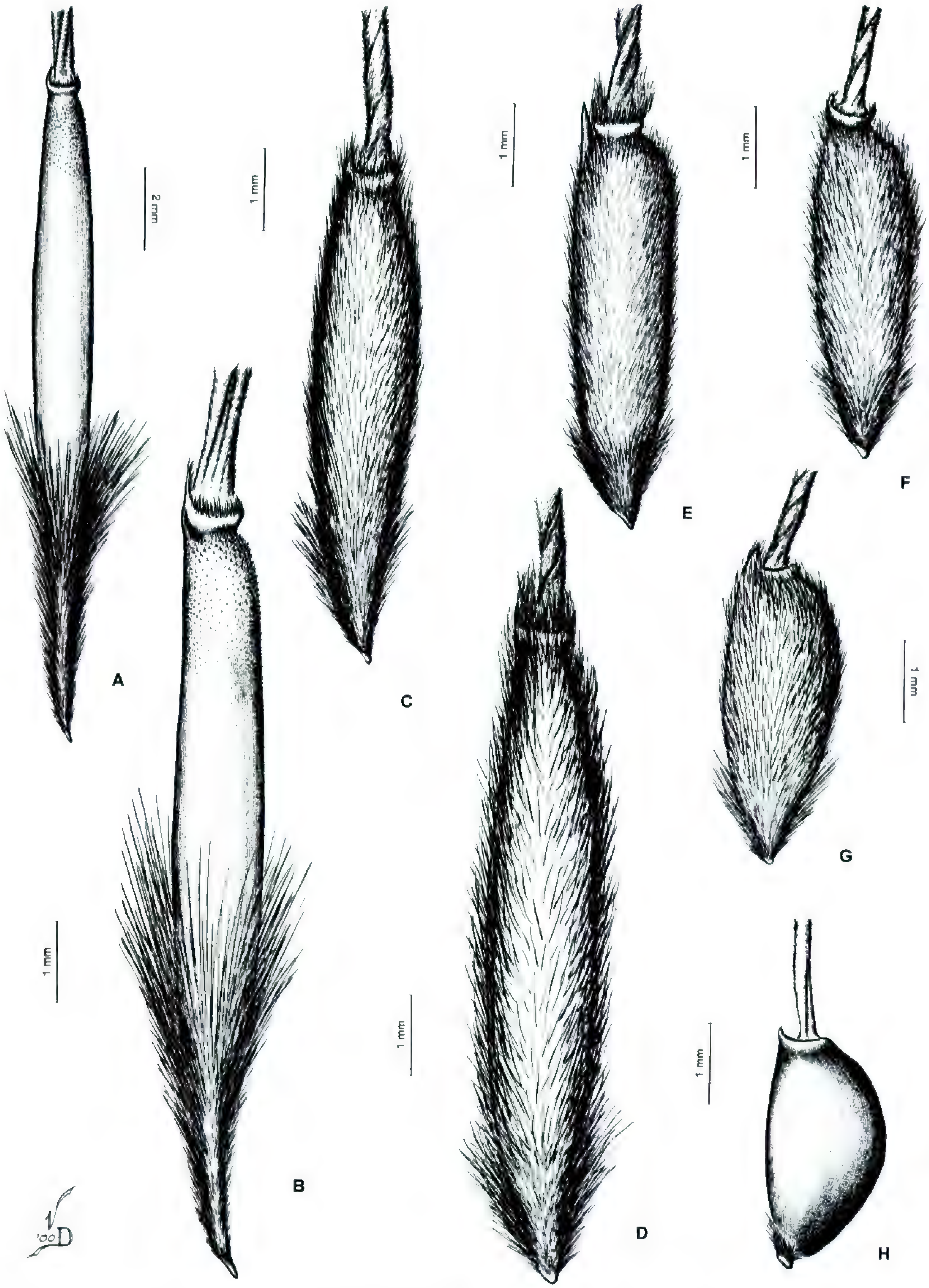

Figure 5. Florets of North American species of *Piptochaetium*.—A. *P. avenacioides* (*Fredholm 5725*). Note that the scale of this drawing is 2 mm. —B. *P. avenaceum* (*Harvey 1854*). —C. *P. virescens* (*King & Soderstrom 5151*). —D. *P. pringlei* (*Pringle 1410*). —E. *P. angustifolium* (*Matuda 29776 a*). —F. *P. seleri* (*Nee & Diggs 24775*). —G. *P. fimbriatum* (*Pringle 8595*). —H. *P. brevicalyx* (*Rzedowski 35863*).

monophyletic group derived from species with cylindrical florets. Species with lens-shaped florets, *P. montevidense* and *P. panicoides*, are derived species within the Obovoid group (Fig. 3). The presence of papillae is another autapomorphy within this small monophyletic group of lens-shaped florets, which is only present in living grasses and never found in fossil taxa studied in this group of Stipeae (Thomasson, 1985).

Piptochaetium angustifolium, *P. fimbriatum*, and *P. seleri* (Fig. 5E, G, and F, respectively) have both plesiomorphic (persistent awns and cylindrical florets) and apomorphic (short and blunt callus) states. As shown by the phylogenetic analyses, these three North and Central American species are intermediate in the evolutionary trend through the Obovoid group.

Distribution patterns of species in *Piptochaetium* suggest that these species found new and different habitats to colonize in South America, with a consequent higher diversification than in the Northern Hemisphere. The monophyletic Obovoid group is mostly South American, except *P. brevicalyx* and *P. montevidense*, which are also present in Mexico, and *P. stipoides* var. *stipoides*, *P. setosum*, and *P. uruguense*, with disjunct distributions in North and South America (Fig. 4). According to Thomasson's suggestions (1980), disjunct species were first widespread along animal migration routes and, later, due to severe climatic fluctuation in the late Tertiary, their distribution became gradually reduced, resulting in relict islands in both hemispheres. Whether species with obovoid florets are derived from species with cylindrical florets in North America or in South America is difficult to determine, as there is no certain evidence for this fact.

Infraspecific Levels

Results from parsimony analyses showed a different origin for subspecies of *P. tovarii*, first recognized by Sánchez Vega (1991). Both subspecies of *P. tovarii* are separated in all cladistic analyses (see NONA and Pee-Wee results, Fig. 3). *Piptochaetium tovarii* subsp. *tovarii*, included herein within the *P. burkartianum* to *P. panicoides* clade, is characterized by the absence of prickles on the lemma surface, while *P. tovarii* var. *pilosa* (= *P. pilosum* herein) is the sister group of the *P. uruguense* to *P. stipoides* var. *echinulatum* clade and does have prickles and macrohairs. Based on these results, the study of type material, and the distribution of characters across the entire genus, there is no reason to keep these entities within the same species. Therefore, *P. tovarii* subsp. *pilosum* is elevated to the rank of species (see the taxonomic treatment herein).

Piptochaetium stipoides is included in the *P. cucullatum* to *P. stipoides* var. *echinulatum* clade (Fig. 4). Relationships between the two varieties of *P. stipoides* were not resolved as much as among the other species of the clade. A possible source of variation within this clade is the polymorphic state of *P. stipoides* var. *stipoides* for several characters principally related with the floret. Moreover, transitional shapes and epidermal characters of the lemma may be variable within a single specimen of this species.

Taxonomic Treatment

Piptochaetium J. Presl, Reliq. Haenk. 1: 222. 1830, nom. cons. *Urachne* Trin. sect. *Piptochaetium* (J. Presl) Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 22. 1842. TYPE: *Piptochaetium setifolium* J. Presl [= *P. panicoides* (Lam.) E. Desv.].

Podopogon Raf., Neogenyton: 4. 1825, nom. rejic. TYPE: *Stipa avenacea* L. (lectotype, designated by Clayton, 1983, not seen).

Caryochloa Spreng., Syst. Veg. 4(2): 22, 30. 1827, hom. illeg., non *Caryochloa* Trinius, 1826. TYPE: *Caryochloa montevidensis* Spreng.

Caespitose, perennial plants. *Culms* herbaceous, unbranched above, erect or somewhat decumbent, terete or slightly flattened, longitudinally striate, glabrous; young shoots intravaginal. *Nodes* compressed, occasionally thickened, the basal nodes slightly geniculate. *Leaf sheaths* generally longer than the internodes at the base, becoming shorter toward the apex. *Ligules* membranous, blunt, usually unfringed. *Leaf blades* linear, convolute to flat, longitudinally striate, frequently glabrous. *Inflorescence* a panicle with branches densely to loosely flowered. *Spikelets* fusiform, laterally compressed to terete, usually long pedicellate, the pedicels unequal in length, generally in pairs, rarely alone toward the apex of the panicle. *Flowers* cleistogamous or chasmogamous. *Glumes* two, persistent, subequal, usually longer than the floret, membranous, lanceolate, acuminate, 3- to 7(8)-nerved, glabrous. *Florets* easily deciduous, terete to laterally compressed. *Lemma* indurate, awned, longitudinally striate, generally with epidermal appendages; lemma margins involute, fitting into the longitudinal groove of the palea; lemma apex fused in a crown, frequently contracted to the base of the awn and with different epidermal appendages. *Awn* usually twice-geniculate, twisted and hispid on the basal portion, straight and shortly scabrous toward the apex, deciduous or persistent. *Callus* acute, subacute or blunt and obliquely truncate, usually hairy, rarely glabrous or subglabrous. *Palea* laterally compressed,

indurate, membranous toward margins, glabrous, shiny and inconspicuously striate, boat-shaped, bikeeled, the apex of the keels projecting as a minute point above the summit of the lemma. *Lodicules* 2 or 3, membranous, blunt or acute, glabrous. *Androecium* of 3 stamens always with short filaments, ca. 0.2 mm long, and small anthers, ca. 0.5 mm long in the cleistogamous flowers, and longer anthers 1–5 mm long in the chasmogamous ones. *Ovary* obovoid, globose to laterally compressed, glabrous, with 2 styles free to their bases; stigmas 2. *Caryopsis* terete to globose or lens-shaped, surface dull, rugose and glabrous, with linear hilum and a small embryo; endosperm hard, without lipid.

KEY TO THE SPECIES OF *PIPTOCHAETIUM*

1a. Florets terete, fusiform or obconical, occasionally fusiform, slightly obovoid; awn robust and persistent; callus usually acute or subacute, rarely blunt.
 2a. Lemma glabrous.
  3a. Lemma with hooks all over surface, decreasing in density toward the callus and the crown .... 10. *P. cabrerai*
  3b. Lemma with hooks and prickles on the upper portion.
   4a. Lemma with inconspicuous hooks .... 25. *P. palustre*
   4b. Lemma with hooks and prickles always conspicuous.
    5a. Floret terete, not gibbous, slightly narrowed below the crown, (6–)9–20 mm long, 1–1.5 mm wide.
     6a. Lower glume 7(8)-nerved; glumes 20–26(–35) mm long; lemma surface dull, with inconspicuous longitudinal striae .... 16. *P. hackelii*
     6b. Lower glume 3(4)-nerved; glumes 15–23 mm long; lemma surface shiny, with conspicuous longitudinal striae.
      7a. Floret (14–)15–20 mm long .... 5. *P. avenacioides*
      7b. Floret (7–)9–12(–13) mm long .... 24. *P. napostaense*
    5b. Floret fusiform, slightly gibbous, or obconical, strongly narrowed below the crown, (3.5–)7.5–11.5(–12) mm long, (0.8–)1.2–2 mm diam.
     8a. Floret fusiform.
      9a. Floret 1.2–1.5 mm wide; lemma with hooks and prickles only below the crown; callus 3.5–4.8 mm long, occasionally shorter .... 12. *P. confusum*
      9b. Floret 1 mm wide; lemma with hooks and prickles on the distal half of the lemma; callus 2–3 mm long .... 4. *P. avenaceum*
     8b. Floret obconical.
      10a. Crown with ascending macrohairs up to 0.6 mm long, conspicuously exceeding the crown in length, sometimes also with a few hooks and prickles.
       11a. Callus 1–2 mm long; floret (3.5–)4.5–6(–7) mm long .... 6. *P. bicolor*
       11b. Callus 2.5–4 mm long; floret (5.5–)7.5–9.5 mm long .... 29. *P. ruprechtianum*
      10b. Crown without macrohairs, with hooks and prickles up to 0.2 mm long, slightly longer than the crown.
       12a. Crown 0.5–0.7 mm diam.; callus 1.2–1.5 mm long; floret (1.2–)1.5–2 mm wide .... 22. *P. medium*
       12b. Crown 0.8–1 mm diam.; callus 1.9–2 mm long; floret 1.2–1.5 mm wide .... 7. *P. brachyspermum*
 2b. Lemma with macrohairs densely disposed all over surface.
  13a. Callus sharp and narrow.
   14a. Inflorescence 3–9 cm long, with 4 to 15 spikelets; spikelets 9–13.5 mm long; Bolivia and Argentina .... 18. *P. indutum*
   14b. Inflorescence longer, 10–30 cm long, with 15 to 80 spikelets; spikelets 5–10 mm long.
    15a. Lower glume shorter than the floret; upper glume as long as the floret; Brazil .... 1. *P. alpinum*
    15b. Both glumes longer than the floret.
     16a. Plants 0.25–0.65 m long; peduncles 8–11.5 cm long; panicles with 15 to 22 spikelets; Peru .... 30. *P. sagasteguii*
     16b. Plants 0.70–1.30 m long; peduncles 40–44 cm long; panicles with 25 to 80 spikelets; Mexico, Guatemala, and Venezuela .... 36. *P. virescens*
  13b. Callus subacute or blunt, always broad.
   17a. Lemma smooth, sometimes a very few hooks present near the crown.
    18a. Floret 7–10 mm long; callus subacute .... 28. *P. pringlei*
    18b. Floret 3.5–5 mm long; callus blunt .... 15. *P. fimbriatum*
   17b. Lemma longitudinally striate, with hooks and prickles all over surface.
    19a. Macrohairs of the lemma, including those of the crown, 1 mm long; floret fusiform .... 3. *P. angustifolium*
    19b. Macrohairs of the lemma, including those of the crown, 0.5 mm long; floret terete, slightly obovoid.

20a. Peduncles 5–14 cm long; inflorescences 3–6.5 cm long, dense; Peru .... 14. *P. featherstonei*
20b. Peduncles 22–26 cm long; inflorescences 7–22 cm long, loose, not dense; Mexico and Guatemala .... 31. *P. seleri*

1b. Florets obovoid or lens-shaped; awn weak and deciduous; callus blunt.
21a. Lemma with many macrohairs.
22a. Macrohairs of the lemma up to 4 mm long, conspicuously longer than the crown .... 20. *P. lasianthum*
22b. Macrohairs of the lemma up to 2 mm long, the upper hairs slightly longer than the crown .... 27. *P. pilosum*
21b. Lemma glabrous.
23a. Awn cone-shaped, base as wide as the crown (0.9–1 mm), glabrous, or occasionally with very few hairs .... 13. *P. cucullatum*
23b. Awn thread-like, shortly hispid, minutely scabrous toward the apex.
24a. Crown 1–1.8 mm diam., not contracted toward the base of the awn.
25a. Callus glabrous, or with few short hairs as long as the callus.
26a. Hooks of the lemma inconspicuously pointed, densely disposed all over the surface, decreasing in size and quantity toward the callus and near the crown .... 11. *P. calvescens*
26b. Lemma with very few hooks, these confined to the distal part toward the crown .... 21. *P. lejopodum*
25b. Callus densely hairy, the hairs exceeding the callus.
27a. Hairs of the callus longer than the floret .... 19. *P. jubatum*
27b. Hairs of the callus one-third or half as long as the floret.
28a. Lemma with prickles partially covered by the edges of adjacent epidermal cells, generally in groups of 2 or 3, uniformly disposed all over the lemma surface, the biggest ones on the middle portion of the floret .... 33b. *P. stipoides* var. *echinulatum*
28b. Lemma with hooks and prickles not covered by the adjacent cells, uniformly disposed on the distal half of the floret, or lemma without epidermal appendages .... 33a. *P. stipoides* var. *stipoides*
24b. Crown 0.4–0.6(–0.9) mm diam., contracted toward the base of the awn.
29a. Lemma with hooks and prickles, densely and uniformly disposed on the distal ¾ of the floret; papillae absent.
30a. Floret globose, sometimes slightly compressed laterally, (1.8–)2.4–3(–3.5) mm long, 0.8–1.2 mm diam.; Paraguay, Uruguay, and northern Argentina .... 35. *P. uruguense*
30b. Floret elongate and conspicuously laterally compressed, (2.5–)3.8–4(–5) mm long, 1–2 mm wide; Chile .... 2. *P. angolense*
29b. Lemma with papillae or with hooks and prickles only below the crown, or lemma without epidermal appendages.
31a. Crown revolute toward the outside .... 33a. *P. stipoides* var. *stipoides*
31b. Crown not revolute.
32a. Floret lens-shaped, conspicuously laterally compressed; lemma and crown with or without papillae.
33a. Lemma with papillae dense and uniformly disposed, decreasing in size and density toward the crown and the callus .... 23. *P. montevidense*
33b. Lemma without papillae, or confined to the region near the crown, on the dorsal side of the floret .... 26. *P. panicoides*
32b. Floret globose to slightly compressed, obovoid, or obconical; lemma and crown with or without hooks, prickles, and macrohairs.
34a. Lemma with a few hooks toward the crown .... 32. *P. setosum*
34b. Lemma without epidermal appendages.
35a. Leaf blades glabrous; floret 2.2–2.5 mm long; callus hairy, the upper hairs ½ the length of the floret .... 9. *P. burkartianum*
35b. Leaf blades hispid on both surfaces, sometimes abaxially glabrous; floret 2.5–3.5 mm long; callus with or without short hairs, the hairs equaling the length of the callus.
36a. Floret obovoid, not gibbous, 0.8–1.2 mm wide .... 34. *P. tovarii*
36b. Floret conspicuously gibbous, 1.5–1.9 mm wide.
37a. Glumes exceeding the length of the floret; lemma dull, with conspicuous longitudinal striae; callus 0.4–0.5 mm long, crown with 1 or 2 rows of hooks and prickles on margin .... 17. *P. hirtum*
37b. Glumes as long as or slightly shorter than the floret; lemma shiny, smooth; callus 0.15–0.25 mm long; crown without epidermal appendages .... 8. *P. brevicalyx*

1. **Piptochaetium alpinum** L. B. Smith, Phytologia 22: 89. 1971. TYPE: Brazil. Santa Catarina: Bom Jardim da Serra, Fazenda da Laranja, 1400 m, *Reitz & Klein 7710* (holotype, US not seen; isotype, HBR not seen).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, up to 1400 m elevation.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

2. **Piptochaetium angolense** Philippi, Anales Univ. Chile 93: 734. 1896. TYPE: Chile. "Angol, Nov. 1887," *Philippi s.n.* (holotype, SGO 057397!).

Distribution. Endemic to central Chile (IV Región).

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

3. **Piptochaetium angustifolium** (Hitchcock) Valencia & Costas, Bol. Soc. Argent. Bot. 12: 177. 1968. *Stipa angustifolia* Hitchc., Contr. U.S. Natl. Herb. 24: 246. 1925. TYPE: Mexico. Coahuila: on summit slope of Sierra de La Puebla in sight of Saltillo, 25 July 1905, *Palmer 726* (holotype, US 570290 not seen; isotypes, BAA Herb. Parodi 2955!, MO!, US 993385 not seen, US 906342 not seen). Figures 2D, 5E.

Plants perennial. *Culms* 10–30 cm tall, glabrous; nodes 2, compressed, glabrous to sparingly pubescent; internodes 3.5–4.5 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 3–4 cm long, glabrous. *Ligules* 1–2 cm long, blunt, margins entire, glabrous. *Leaf blades* linear, convolute, 9–10(–20) cm long, 0.5–0.6 mm wide, longitudinally striate, glabrous. *Peduncles* terete, slightly flattened, 7–10 cm long, longitudinally striate, glabrous. *Inflorescences* 6.5–7.5 cm long, few-flowered (8 to 18 spikelets), with branches loosely disposed; pedicels 2–7 mm long, scabrous. *Spikelets* fusiform, 6–6.5 mm long, 1 mm diam. *Glumes* longer than the floret, subequal, 6–6.5 mm long, shortly acuminate, 5-nerved, greenish, hyaline toward the margins. *Floret* fusiform, 4.5–5 mm long, 0.9–1 mm diam. *Lemma* 4.5–5 mm long, contracted below the crown, longitudinally striate, densely pilose, with macrohairs 1 mm long, hooks and prickles all over surface; crown contracted at the base of the awn, 0.4–0.5 mm diam., straight, not revolute, with densely disposed prickles and macrohairs, the latter 1 mm long, persistent; callus 0.6–1 mm long, subacute, densely pilose, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 10–11 mm long, persistent, scabrous along length. *Palea* 4 mm long. *Lodicules* 2, 1 mm long, blunt. *Caryopsis* not seen.

Distribution. This species is known only from northeastern and eastern Mexico, in the states of Coahuila, Nuevo León, and Mexico, up to 3500 m.

Additional specimens examined. MEXICO. **México:** C. Pelon de Ñado, 2700–3500 m, *Matuda et al. 29776* (US). **Nuevo León:** Hacienda Vista Hermosa, 35 mi. S of Monterrey, 810 m, 25 June 1939, *Harvey 1038* (US).

Piptochaetium angustifolium is similar to *P. featherstonei* and *P. seleri*, but these species differ in having short, 0.5 mm, macrohairs on the lemma and crown, and a terete, slightly obovoid floret.

4. **Piptochaetium avenaceum** (L.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 229. 1944. *Stipa avenacea* L., Sp. Pl. 1: 78. 1753. TYPE: U.S.A. Virginia: *Clayton 621* (lectotype, designated by Clayton (1983), LINN-94.5 not seen; isolectotype, BM not seen). Figures 2C, 5B.

Stipa barbata Michx., Fl. Bor.-Amer. 1: 53. 1803, nom. illeg., non *Stipa barbata* Desf., Fl. Atlant. 1: 97. 1798. *Stipa virginica* Pers., Syn. Pl. 1: 99. 1805. *Podopogon barbatus* Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. TYPE: U.S.A. "In sylvis Virginiae Carolinae," *Michaux s.n.* (holotype, P not seen; isotype, US not seen).

Stipa avenacea var. *bicolor* Eaton & J. Wright, Man. Bot. (ed. 8): 444. 1848. TYPE: "United States of America" (not located).

Stipa leiantha Hitchc., Contr. U.S. Natl. Herb. 24: 236. 1925. *Piptochaetium leianthum* (Hitchc.) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico. Puebla: 2600 m, *Hitchcock 6489* (holotype, US 993443 not seen).

Piptochaetium avenacellum Barkworth, Syst. Bot. 13: 196. 1988. TYPE: Mexico. Tamaulipas: 4 km W of Miquihauan, 23°42′N, 99°45′W, on limestone ridges in open pine forest, 3110 m, 4 Aug. 1941, *Stanford et al. 645A* (holotype, US not seen; isotype, MO not seen).

Plants perennial. *Culms* (30–)50–80 cm tall, glabrous; nodes 2–3, yellowish to reddish, compressed, glabrous; internodes 5–25 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, (4–)6–16 cm long, glabrous. *Ligules* 2–3 mm long, subacute to blunt, margins entire, glabrous. *Leaf blades* linear, convolute, occasionally flat, 8–30 cm long, 0.8–0.9 mm wide, adaxial side conspicuously striate, glabrous or scabrous, margins shortly scabrous. *Peduncles* terete, slightly flattened, 8–10 cm long, longitudinally striate, gla-

brous. *Inflorescences* 15–22 cm long, few-flowered (10 to 15(–25) spikelets), with branches loosely disposed; pedicels flattened, 1.5–5 cm long, hispid. *Spikelets* fusiform, 10–12 mm long, 1–1.2 mm diam. *Glumes* subequal, longer than the floret, 10–12(–15) mm long, acute, lower glume 3(5)-nerved, upper glume 5-nerved. *Floret* terete-fusiform, slightly compressed, (7–)9–12(–13) mm long, 1 mm diam. *Lemma* contracted below the crown, 9–12(–13) mm long, thinly striate, with hooks and prickles toward the distal portion (1/3–2/3 of the surface); crown contracted at the base of the awn, straight, not revolute, 0.5–0.6 mm diam., with prickles and macrohairs up to 0.5 mm long, occasionally up to 1 mm long; callus ca. 2 mm long, sharp, hairy, the upper macrohairs reaching ⅓–½ the length of the floret; awn bigeniculate, 5–7 cm long, persistent, hispid, scabrous toward the apex. *Palea* 7–8 mm long. *Lodicules* 2, 1.5 mm long, acute. *Caryopsis* terete, 5.5–6 mm long, 0.5–0.6 mm diam.; hilum linear; embryo ⅕ the length of the caryopsis.

Chromosome numbers. 2*n* = 22, 28 (Gould, 1958, as *Stipa avenacea* L.); n = 11 (Valencia & Costas, 1968).

Distribution. Widespread in the eastern and southern United States and northeastern Mexico.

Additional specimens examined. U.S.A. **Alabama:** Marshall Co., margin of a woodland, along Alabama 240, about 10 mi. E of Morgan City, *Henderson 91-3* (MO); Lee Co., Auburn, *Earle & Baker s.n.* (US 344773). **Arkansas:** Garland Co., 30 Apr. 1939, *Demaree 19003* (US); Coastal Plain Region, *Demaree 63483* (MO). **Connecticut:** New Haven Co., dry ledgy places toward summit of Mt. Carmel, *Weatherby 5831* (US). **Florida:** Wakulla Co., St. Marks Wildlife Refuge, *Godfrey 67795* (US); Highlands Co., waste area just W of Sebring, *Deam 64413* (US); Gainesville, *Garber s.n.* (US 992485). **Georgia:** Ben Hill Co., 16.3 mi. ENE of Fitzgerald, *Faircloth 5079* (MO); Glynn Co., N end of Jekyll Island, *Strong 1342* (US); Walker Co., near summit of ridge near Maddox Gap, between Villanow and La Fayette, *Cronquist 4432* (US). **Indiana:** N side of the Pidgeon River about 3 mi. SE of Mongo, *Deam 40704* (US). **Louisiana:** Pipeline off La. 507, 3 mi. W of Bienville, *Larrick 249* (BAA); roadside about 2 mi. NE of Mansfield, *Thieret 28558* (US). **Maryland:** region of Marlboro, *Hitchcock 12616* (US). **Massachusetts:** Barnstable Co., *Hoffmann s.n.* (MO); Tisbuty, *Seymour 1060* (US); just E of hwy. 28, near junction with hwy. 138, Blue Hill Reservation, SE of Boston, *Reeder & Reeder 233* (US). **Michigan:** 6 mi. W of Richland at Spring Brook and railroad, *Harvey 1764* (SI); Kalamazoo Co., Sect. 36, 2 mi. S of Alamo, *Harvey 1854* (BAA, US). **Mississippi:** Lowndes Co., just W of Mayhew junction on ridge, *McDaniel 1811* (MO); Wayne Co., Bucatunna, *Jacob 815* (US). **New Jersey:** near Jenkins, Wharton State Forest, Pine Barrens, *Harkins 809* (MO); Atlantic Co., *Chase 7312* (US). **New York:** Eastport, Long Island, *Chase 7401* (US). **North Carolina:** Wake Co., Lake Johnson, 4 mi. SW of Raleigh, *Godfrey 3686* (US); Durham Co., wooded slope, *Simpson s.n.* (US 2479778). **Oklahoma:** Le Flore Co., near state line on hwy. 63, E of Big Cedar, *Waterfall 14854* (US). **Pennsylvania:** s.l., *Scribner 266* (US). **Rhode Island:** Providence Co., *Collins s.n.* (US 1912039). **South Carolina:** Laurens Co., side of U.S. 276, just SE of Ora, *Iltis 23032* (MO); Horry Co., S of Myrtle Beach, *Griscom 16409* (US); McCormick Co., 1 mi. NE of Savannah River on SC hwy. 28, *Bozeman & Radford 8842* (US). **Tennessee:** Marion Co., 9 mi. SE of Tracy City, *Kral 46479* (MO); Roane Co., last slope of Cumberland Plateau, W of Rockwood, *Weatherby 6234* (US). **Texas:** Jasper Co., 8 mi. SE of Jasper, hwy. 190, *Shinners 7029* (SI); Shelby Co., sandy scrub oak land 7 mi. S of Center, *Correll 16170* (US). **Virginia:** Accomac Co., Chincoteague Island, *Gleason 8537* (US); Hampton, dry open woods, *Miller Jr. s.n.* (US 646829). **West Virginia:** on wooded hillside near Reymon Memorial farm, Wardensville, *Berkley 1579* (MO). MEXICO. **Tamaulipas:** 3 mi. N of Miquihauana, *Stanford et al. 2482* (US, paratype of *Piptochaetium avenacellum*).

Piptochaetium avenaceum resembles *P. confusum* and *P. napostaense*, as they share the shape of the floret and the appendages (prickles and hooks) on the lemma and crown, but they are distinguished as follows: in *P. avenaceum*, the prickles and hooks are distributed on the distal portion, sometimes reaching half the length of the floret. In *P. confusum* and *P. napostaense* such appendages occur only immediately below the crown. Both *P. avenaceum* and *P. napostaense* have florets that are 1 mm in diameter, but the callus length is 2–3 mm long in *P. avenaceum* and 3.5–6 mm in *P. napostaense*. *Piptochaetium confusum* has florets 1.2–1.5 mm in diameter with a callus 3.5–4.8 mm long.

5. Piptochaetium avenacioides (Nash) Valencia & Costas, Bol. Soc. Argent. Bot. 12: 175. 1968. *Stipa avenacioides* Nash, Bull. Torrey Bot. Club 22: 423. 1895. TYPE: U.S.A. Florida: Lake Co., in pine lands near Cassia, 16/30 June 1895, *Nash 2051* (holotype, NY not seen; isotypes, BAA!, MO!, US!). Figure 5A.

Plants perennial. *Culms* 0.70–1.20 m tall, glabrous or pubescent below the basal nodes; nodes yellowish, glabrous; internodes 15–25 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 7–20 cm long, glabrous. *Ligules* 1–3 mm long, blunt or acute, margins entire, glabrous. *Leaf blades* linear, convolute, 15–30 cm long, 1 mm wide, longitudinally striate, glabrous. *Peduncles* terete, 22–25 cm long, longitudinally striate, glabrous. *Inflorescences* 10–30 cm long, few- to many-flowered (10 to 50 spikelets), with branches loosely disposed; pedicels 1.5–2 cm long, scabrous. *Spikelets* fusiform, 18–22 mm long, 1–2 mm diam. *Glumes* longer than the floret, 18–22 mm long, acuminate, (3)5-nerved. *Floret* terete, (14–)15–20 mm long, 1–1.2 mm diam. *Lemma* 15–20 mm long, contracted below the crown, longitudinally striate, with

small hooks on the distal portion (1/3–2/3 of the surface); crown contracted at the base of the awn, 0.6–0.7 mm diam., with hooks, prickles, and macrohairs 0.4–0.5 mm long, persistent; callus 6–8 mm long, acute, densely hairy; awn bigeniculate, persistent, 8–12 mm long, hispid at the basal portion, scabrous toward the apex. *Palea* 12 mm long. *Lodicules* 2, ca. 2.5 mm long, acute. *Caryopsis* not seen.

Distribution and ecology. Only known from the United States, in Florida. This species grows in dry and sandy places.

Additional specimens examined. U.S.A. **Florida:** Brevard Co., *Fredholm 5725* (BAA, MO, US); Eau Gallie, *Curtiss 5834* (MO, US); Orange Co., Mermiack, *Baker 115* (US); Manatel Co., Palma Sola, *Tracy 7031* (MO, US); Duval Co., *Fredholm 5092* (US); W of Tavares, *Hitchcock 812* (US); Braidentown, *Hitchcock 967* (US); s.l., *Dowell 7309* (BAA, US); Orange Co., Clarcona, *Meislahn 191* (US).

6. Piptochaetium bicolor (Vahl) E. Desvaux, Fl. Chil. 6: 273. 1853. *Stipa bicolor* Vahl, Symb. Bot. 5(2): 24. 1791. *Oryzopsis bicolor* (Vahl) Speg., Anales Mus. Nac. Montevideo 4(2): 6. 1901. *Piptochaetium bicolor* var. *typicum* Parodi, Revista Mus. La Plata 6(25): 252. 1944, nom. inval. TYPE: Uruguay. "Habitat in Brasiliae Monte Video. *Dn. Thouin*," Herb. Vahl, IDC microfiche photo Vahl, nr. 73 III, 4–5 (holotype, C!).

Stipa intermedia Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 26. 1842. TYPE: Brazil. "Brasilia meridionalis," *Sellow δ 784* (holotype, LE not seen; isotypes, US!, B not seen).

Stipa megalantha Steud., Syn. Pl. Glumac. 1: 124. 1854. TYPE: Chile. Valparaíso, Concon, Nov. 1829, *Herb. Steudel* (holotype, P!).

Oryzopsis bicolor (Vahl) Speg. var. *minor* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. *Piptochaetium bicolor* (Vahl) E. Desv. var. *minor* (Speg.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 256. 1944. TYPE: Argentina. Buenos Aires: Bavio, Estancia Elizalde, *Spegazzini s.n.* (holotype, LPS 12513! sheet A; isotype, LPS 12513! sheet B).

Distribution. Central Chile, in V Región, western and southern Uruguay in the departments of Canelones, Florida, Montevideo, and San José, and central eastern Argentina in the provinces of Buenos Aires and Entre Ríos.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

7. Piptochaetium brachyspermum (Spegazzini) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 241. 1944. *Oryzopsis napostaensis* Speg. var. *brachysperma* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Carmen de Patagones, *Spegazzini 42 b* (holotype, LPS 2471!).

Distribution. Endemic to Argentina, where it is only known from the southern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

8. Piptochaetium brevicalyx (E. Fournier) Ricker, Contr. U.S. Natl. Herb. 17: 286. 1918. *Stipa brevicalyx* E. Fourn., Mexic. Pl. 2: 150. 1886. TYPE: Mexico. San Luis Potosí: cerca de San Luis Potosí, 6000–8000 ft., 1878, *Parry & Palmer 959* (holotype, US not seen; isotypes, BAA!, K not seen, MO not seen, NY not seen). Figures 1A, 2A, 5H.

Piptochaetium brevicalyx (E. Fourn.) Ricker subsp. *flexuosum* Barkworth, Syst. Bot. 13: 200. 1988. TYPE: Mexico. Durango: 65–75 km W of Durango City on road to La Flor, 2620 m elevation, *Breedlove 44215* (holotype, CAS 622475 not seen).

Plants perennial. *Culms* (6–)10–50 cm tall; nodes 3 or 4, compressed, reddish, glabrous; internodes 2–12 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, 2–5 cm long, glabrous to scabrous. *Ligules* 0.6–1.2 mm long, blunt to subacute, margins entire or fringed, glabrous. *Leaf blades* linear, convolute or flat, 5–30 cm long, 0.6–1.2 mm wide, glabrous or hispid. *Peduncles* terete, 2.5–7 cm long, longitudinally striate, glabrous. *Inflorescences* 3–10 cm long, few-flowered (5 to 20 spikelets), with branches densely disposed; pedicels 2–8 mm long, glabrous or hispid. *Spikelets* globose, 2.5–3.5 mm long, 1.5–1.7 mm diam. *Glumes* subequal, shortly acuminate, violet-colored, hyaline toward the margins, 5- or 7-nerved; lower glume slightly shorter than the floret, 2.4–3.3 mm long; upper glume shorter than or as long as the floret, 2.4–3.5 mm long. *Floret* globose, slightly compressed, gibbous, 2.5–3.5 mm long, 1.5–1.9 mm wide. *Lemma* contracted below the crown, 2.5–3.5 mm long, smooth, shiny, without epidermal appendages; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.5–0.7 mm diam., without epidermal appendages; callus 0.15–0.25 mm long, blunt, obliquely truncate, with few, occasionally many, short hairs; awn slightly geniculate to almost straight, 6–18 mm long, hispid, scabrous toward the apex, deciduous. *Palea* 2.5–3.7 mm long. Lodicules 2, 1 mm long, acute. *Caryopsis* not seen.

Distribution. Central Mexico, up to aproximately 3000 m.

Additional specimens examined. MEXICO. **Durango:** 5.3 km W of (Ejido) Los Mimbres turnoff, *Iltis et al. 214* (US); 41 km NE of El Salto, *Mick & Roe 87* (US! paratype

of *P. brevicalyx* subsp. *flexuosum*). **Guanajuato:** 10 km al sur de Ibarra, Ocampo, sobre la carretera a León, *Rzedowski 50768* (MEXU). **Hidalgo:** 8 km al noreste de Pachuca, sobre la carretera a Real del Monte, *Rzedowski 35863* (MEXU, XAL); Cerro Ventoso, above Pachuca, *Pringle 7606* (MEXU); in oak woods near Real del Monte, *Rose et al. 8680* (US); Pachuca, *Hitchcock 6733* (US). **México:** rocky roadcut, 27 mi. S of San Juan del Río, *Gould 9211* (US). **San Luis Potosí:** Cerro La Bolsa, W de Cerrito de Dolores, Mun. Villa de Arriaga, *Banda et al. 132* (CAS, MO); near Cerro Prieto, *Sohns 1535* (US). **Tlaxcala:** between San Cristóbal and Calpulalpan, *Sohns 553* (MEXU, US).

Piptochaetium brevicalyx is similar to *P. hirtum*: both species share the globose floret shape, the absence of epidermal appendages on the lemma, and generally few hairs on the callus. They can be recognized because *P. hirtum* presents conspicuous longitudinal striae on the dull lemma surface, 1 or 2 rows of hooks or prickles in the crown, and both glumes 5.5–6 mm, longer than the floret.

Barkworth (1988) recognized *Piptochaetium brevicalyx* subsp. *flexuosum* based on the relatively long and widespread branches of the inflorescences. Although there are specimens with dense or extended panicles, the difference between the length of the branches is slight, and, within the studied material, there are specimens with both types of inflorescences, such as *Banda et al. 132*.

9. Piptochaetium burkartianum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 291. 1944. TYPE: Argentina. Corrientes: San Martín, La Cruz, Nov. 1936, *Parodi 12329 1/2* (holotype, BAA!).

Distribution. Endemic to Argentina; only found in the eastern province of Corrientes, at the type locality.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

10. Piptochaetium cabrerae Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 243. 1944. TYPE: Argentina. Buenos Aires: Puan, Villa Iris, 7 Nov. 1940, *Parodi 13771* (holotype, BAA!).

Distribution. Endemic to Argentina; only collected in the southwestern province of Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

11. Piptochaetium calvescens Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 278. 1944. TYPE: Argentina. Prov. Buenos Aires: Sierra Currumalán, 600 m s.m., 10 Nov. 1932, *Parodi 10343* (holotype, BAA!).

Distribution. Central and eastern Argentina in the province of Buenos Aires, and southern Uruguay in the department of Montevideo.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

12. Piptochaetium confusum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 246. 1944. TYPE: Argentina. Entre Ríos: Concordia, 3 Nov. 1921, *Parodi 3950* (holotype, BAA!).

Distribution and ecology. Uruguay in the departments of Maldonado, Montevideo, and Paysandú, and central eastern Argentina in the province of Entre Ríos. This species grows in dry grasslands and rocky places.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

13. Piptochaetium cucullatum Rosengurtt & Izaguirre de Arturio, Bol. Univ. Rep. Fac. Agron. Montevideo 90: 3. 1966. TYPE: Uruguay. Dpto. Salto: Termas del Arapey, próximo a la Estación, 9 Dec. 1962, *Arrillaga et al. 1512* (holotype, MVFA not seen; isotypes, BAA!, US 2951786 not seen).

Distribution. Endemic to northern Uruguay in the departments of Salto and Paysandú.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

14. Piptochaetium featherstonei (Hitchcock) Tovar, Opusc. Bot. Pharm. Complut. 4: 104. 1988. *Stipa featherstonei* Hitchc., Proc. Biol. Soc. Wash. 36: 196. 1923. TYPE: Peru. Río Blanco, 4500 m, 8–19 May 1922, *J. F. Macbride & W. Featherstone 803a* (holotype, F 517331 pro parte not seen; isotype, US not seen).

Piptochaetium juninense Tovar & Gutte, Feddes Repert. Spec. Nov. Regni Veg. 91(4): 205. 1980. TYPE: Peru. Junín: Prov. Yauli, La Oroya, Berg oberhalb Pachacayo (Puya raimondii-Vorkommen), Steiniger Abhang, Hohe, 3750 m, *Gutte 2130* (holotype, LZ not seen; isotypes, SMF not seen, USM!).

Distribution. Southwestern Peru in the departments of Ancash, Ayacucho, and Junín at elevations between 3000 and 4500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. Hitchcock (1923) mentioned that the holotype is mounted with plants of *Stipa hansmeyeri*, but, according to Soreng (pers. comm.), it is not clear if that specimen was subdivided into parts a and b by the collectors or by Hitchcock

himself; the US isotype has only *Stipa featherstonei* on it.

15. Piptochaetium fimbriatum (Kunth) Hitchcock, J. Wash. Acad. Sci. 23(10): 453. 1933. *Stipa fimbriata* Kunth, Nov. Gen. Sp. 1: 126. 1816. *Oryzopsis fimbriata* (Kunth) Hemsl., Biol. Cent.-Amer., Bot. 3: 538. 1885. TYPE: Mexico. Guanaxuato, Billalpando, *Humboldt & Bonpland s.n.*, Herb. HBK 4224 (holotype, P not seen; isotype, BAA!). Figures 2B, 5G.

Piptochaetium fimbriatum (Kunth) Hitchc. var. *confine* I. M. Johnst., J. Arnold Arbor. 24: 396. 1943. TYPE: Mexico. Coahuila: Sierra del Pino, La Noria, *Johnston & Mueller 486* (holotype, GH not seen; isotype, LL not seen).

Plants perennial. *Culms* 35–80 cm tall, glabrous, sometimes pubescent below the nodes; nodes 2–3, slightly compressed or enlarged, reddish, glabrous; internodes 6–11 cm long. *Leaf sheaths* tightly embracing the culms, shorter than the internodes, (3–)5–8 cm long, glabrous. *Ligules* 1.5–2 mm long, acute, glabrous. *Leaf blades* linear, convolute or flat, 6–26 cm long, 0.9–1.1 mm wide, adaxial side conspicuously striate, glabrous on both faces, margins scabrous. *Peduncles* terete, 12–28 cm long, longitudinally striate, glabrous. *Inflorescences* 14–20 cm long, many-flowered (20 to 60 spikelets), with branches loosely disposed; pedicels flattened, 4–12 mm long, hispid. *Spikelets* fusiform to slightly obovoid, 3.5–5 mm long, 1 mm diam. *Glumes* subequal, longer than the floret, 4–6 mm long, shortly acuminate, 5- or 7-nerved. *Floret* fusiform, slightly obovoid and gibbous, 3.5–5 mm long, 1.2–1.8 mm diam. *Lemma* contracted below the crown, 3.5–5 mm long, smooth, shiny, with deciduous macrohairs, densely disposed; crown contracted at the base of the awn, inconspicuous, straight, not revolute, ca. 0.8 mm diam., without epidermal appendages; callus 0.2–0.5 mm long, blunt, obliquely truncate, hairy, the upper macrohairs reaching ⅕ the length of the floret; awn bigeniculate, 10–20 mm long, persistent, hispid to scabrous. *Palea* 3.5–3.6 mm long. *Lodicules* 2, ca. 1 mm long, subacute. *Caryopsis* fusiform, 2.5 mm long, 0.6 mm diam.; hilum linear; embryo 1/5 the length of the caryopsis.

Chromosome numbers. $2n = 44$ (Brown, 1951); $n = 21$ (Reeder, 1968); $2n = 44$ (Valencia & Costas, 1968).

Distribution. Widespread in the southern and southeastern United States and Mexico, at elevations between 1900 and 2500 m. This species has also been cited for Guatemala, in the department of Huehuetenango (Swallen, 1955; Beetle, 1977).

Additional specimens examined. U.S.A. **Arizona:** Santa Cruz Co., Canelo Hills, along road 1.5 mi. N of Canelo Pass, *Toolin & McHargue 2222* (MO); Patagonia Mts., *Kearney & Peebles 10114* (US); Cochise Co., Cave Creek Chiricahua Mountains, *Peterson & Annable 4010* (MO, US). **New Mexico:** Grant Co., Bear Mt., near Silver City, *Metcalfe 746* (US); San Miguel Co., 8.5 mi. S of Rte. 104, 15 mi. E of Las Vegas, *Hill 14632* (MO); Santa Rita Mt., Grant Co., *Metcalfe 1471* (MO, US). **Texas:** J. Davis Co., 6.8 mi. on road to "Davis Mt. Resort" (Tomahawk trail) from State Hwy. 166, 1770 m, *Brant et al. 2239* (MO); Brewster Co., rocky slope near summit of Mt. Emory, Chisos Mts., *Correll 13699* (US); Chisos Mountains, Brewster Co., 1 mi. SW of Boot Spring, 2120 m, *Moore & Steyermark 3172* (MO, US). MEXICO. **Baja California Sur:** granitic slopes surrounding long interior valley (La Laguna), S of Pico La Aguja on the Sierra La Laguna, *Breedlove & Axelrod 43293* (MO). **Chiapas:** Teopisca, Belém, 8 km NW of Teopisca along hwy. to San Cristóbal de las Casas, *Davidse et al. 29775* (MEXU). **Chihuahua:** foothills of Sierra Madre, *Pringle 3035* (MEXU); Miñacam, *Hitchcock 7741* (US). **Coahuila:** Buenavista, Saltillo, Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Madrigal A. s.n.* (XAL); Cañón San Lorenzo, 5 km de Saltillo hacia Zacatecas, *Serrato Sánchez s.n.* (MEXU 309021). **Distrito Federal:** Cima de Toluca, *Lyonnet 48* (MO). **Durango:** on top of rugged volcanic plateau 5.3 km W of (Ejido) Los Mimbres turnoff al km 54.2 WSW of Durango and ca. halfway to El Salto, *Iltis et al. 213* (XAL). **Guanajuato:** ca. 8 km W of San Felipe, *Sohns 424* (MO, US). **Hidalgo:** open pine woods near Ocotillos between Comanche and Huasca, ca. 2200 m, *Moore & Wood Jr. 4164* (US). **Jalisco:** Mezquitic, 8 km SE del Rancho El Mortero, *Rzedowski 17704* (US). **México:** Tezcoco, lado sur de la Cañada de Aguas, 13.5 km al SE de Tezcoco, 11 km al ESE de Coatlinchán, *Koch 77110* (MEXU); roadside, old hwy. 190 between turnoff to Chalco (Hwy. 115), Santa Bárbara ca. 30 m above Azotla, *Mick & Roe 287* (XAL). **Michoacán:** 0.6 mi. E of Poblado Constitution, *Kral 25586* (MO); ca. 20 mi. W of Morelia, *Sohns 782* (US). **Nuevo León:** 28.6 mi. N of La Ascencion on Mex 60, *Brunken & Perino 234* (MO). **Oaxaca:** 7 km N de Amatlán, Nochixtlán, *Mendoza & Mérica 2640* (MO). **Puebla:** Tepeyahualco, *Calzada et al. 4645* (XAL); vicinity of San Luis Tultilanapa, *Purpus 3589* (US). **San Luis Potosí:** Cerro La Laderona, 2.5 km S de La Amapola, Escalerillas, *Zavala Ch. 862* (XAL); in canyons in the Sierra de San Miguelito, ca. 2 km W of Terrero, 1850–2200 m, 8 Sep. 1954, *Sohns 1147* (US). **Sonora:** Sierra de los Ajos, Rancho de los Ajos, Cañón de Evans, *Felger et al. 92-794* (MO). **Tamaulipas:** Marcella, *Stanford et al. 2604* (MO). **Tlaxcala:** between San Cristóbal and Capulalpan in open, lightly wooded areas, *Sohns 581* (MEXU); Contadero, *Pringle 8595* (MEXU). **Zacatecas:** 9.5 mi. W of Sombrerete, *Taylor & Taylor 6254* (US).

The epidermal surfaces of the lemma in *Piptochaetium fimbriatum* and *P. pringlei* are similar, as both species present smooth and shiny floret surfaces with the macrohairs deciduous. However, *P. pringlei* differs in having bigger florets, from 7 to 10 mm long, and a subacute callus.

16. Piptochaetium hackelii (Arechavaleta) Parodi, Revista Fac. Agron. Veterin. 7(1): 162. 1930. *Stipa hackelii* Arechav., Anales Mus. Nac. Hist. Nat. Buenos Aires 4: 179. 1895. *Oryzopsis hackelii* (Arechav.) Speg., Anales Mus. Nac. Montevideo 4(2): 10. 1901. *Piptochaetium hackelii* (Arechav.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Cerro de Montevideo, cerca de la cumbre, *Arechavaleta 39 a* (holotype, not located; isotype, LPS 2486!, US not seen).

Stipa tandilensis Kuntze, Rev. Gen. Pl. 3(2): 373. 1898. TYPE: Argentina. Buenos Aires: Tandil, Nov. 1892, *Otto Kuntze s.n.* (holotype, NY!).

Distribution. This species grows in the grasslands of Uruguay in the departments of Lavalleja, Maldonado, and Río Negro, as well as in central Argentina in the provinces of Buenos Aires and La Pampa.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. The holotype of *Stipa hackelii* Arechav. could not be located. According to Alonso Paz (pers. comm.), Arechavaleta did not choose types, so in many cases a lectotype must be designated.

17. Piptochaetium hirtum Philippi, Anales Univ. Chile 43: 559. 1873. TYPE: Chile. Cerro de Renca, Dec. 1864, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45078!; isolectotypes, K!, SGO 57422!).

Piptochaetium brevifolium Phil., Anales Univ. Chile 93: 733. 1896. TYPE: Chile. Cerro de Renca, 11 Nov. 1877, *Philippi s.n.* (lectotype, designated by Cialdella & Arriaga (1998), SGO 45077!; isolectotypes, SGO 45078!, SGO 57421!).

Distribution. Known from Cerro de Renca in Chile and San Martín de los Andes in the province of Neuquen in Argentina (Parodi, 1961).

For a description and illustrations, see Cialdella and Arriaga (1998).

18. Piptochaetium indutum Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 258. 1944. TYPE: Argentina. Salta: Rosario de Lerma, Puerta Tastil, 2700 m, *Venturi 8414* (holotype, US not seen; isotype, BAA!).

Distribution. Originally known from northern Argentina from the provinces of Salta and Jujuy, distributed in Bolivia in the departments of La Paz and Potosí, central western Peru in the departments of Ancash, La Libertad, and Lima, between 2500 and 4500 m; it is also cited from Ecuador in the province of Azuay (Jørgensen & León-Yánez, 1999).

Additional specimens examined. PERU. **Ancash:** Recuay Prov., Huascaran Nat. Park, Río Pachacoto, *Smith & Torres 11794 A* (MO); Yungas Prov., Huascarán National Park, Llanganuco Sector, *Smith 10488* (MO); Recuay Prov., Quebrada Huanca, *Smith & Buddensiek 10964* (MO). **La Libertad:** Sánchez Carrion Prov., Trujillo–Huamachuco road, 20 km W of Huamachuco, *Smith & Vásquez M. 3327* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

19. Piptochaetium jubatum Henrard, Recueil Trav. Bot. Néerl. 36: 537. 1939. TYPE: Uruguay. Canelones: Río Santa Lucía, Paso Cuello, *Gallinal et al. 2198* (holotype, Herb. Lugd. Bat. n. 938.280–383, L!; isotypes, US 1723425 not seen, BAA!).

Distribution. Known only from the department of Canelones in Uruguay.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

20. Piptochaetium lasianthum Grisebach, Symb. Fl. Argent.: 297. 1879. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, Quinta del Colegio, en praderas, *Lorentz s.n., Flora Entrerriana n. 1157* (holotype, not located; isotype, CORD!).

Piptochaetium erianthum Balansa, Bull. Soc. Bot. France 32: 244. 1885. TYPE: Uruguay. Cerro de Montevideo, 1874, *Balansa 9* (holotype, not located).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, central and southern Uruguay in the departments of Flores, Lavalleja, and Montevideo, and widespread in central eastern Argentina in the provinces of Buenos Aires, Córdoba, Corrientes, Entre Ríos, Misiones, and Santa Fe.

Additional specimen examined. ARGENTINA. **Misiones:** Candelaria, Villa Venecia, *Renvoize et al. 3025* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

21. Piptochaetium lejopodum (Spegazzini) Henrard, Recueil Trav. Bot. Néerl. 36: 536. 1939. *Oryzopsis lejopoda* Speg., Anales Mus. Nac. Montevideo 4(2): 19. 1901. TYPE: Argentina. Buenos Aires: Sierra de la Ventana, Valle de las Vertientes, Nov. 1895, *C. L. Spegazzini s.n.* (holotype, LPS 12666!).

Distribution. Southern Uruguay in the depart-

ments of Lavalleja and Maldonado, and central eastern Argentina in southern Buenos Aires.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

22. Piptochaetium medium (Spegazzini) Torres, Bol. Soc. Argent. Bot. 11(4): 251. 1969. *Oryzopsis bicolor* (Vahl) Speg. var. *media* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini s.n.* (lectotype, designated by Torres (1969), LPS 12517!).

Distribution. Southern Brazil in the state of Rio Grande do Sul, southern Uruguay in the department of Florida, and eastern Argentina, widespread in the provinces of Buenos Aires, Córdoba, Entre Ríos, La Pampa, Misiones, and Santa Fe.

Additional specimens examined. BRAZIL. **Rio Grande do Sul:** Esmeralda, 29 Nov. 1988, *M. Sallés 141, 142* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

23. Piptochaetium montevidense (Sprengel) Parodi, Revista Fac. Agron. Veterin. 7(1): 163. 1930. *Caryochloa montevidensis* Spreng., Syst. Veg. 4(2): 30. 1827. *Oryzopsis montevidensis* (Spreng.) Hauman, Anales Mus. Nac. Hist. Nat. Buenos Aires 29: 116. 1917. *Oryzopsis montevidensis* (Spreng.) Speg., Revista Argent. Bot. 1(1): 10. 1925, comb. superfl. *Oryzopsis montevidensis* (Spreng.) Speg. f. *typica* Speg., Revista Argent. Bot. 1(1): 11. 1925, nom. inval. *Piptochaetium montevidense* (Spreng.) Herter, Estud. Bot. Reg. Urug. 4: Florula Urug.: 34. 1930, comb. superfl. TYPE: Uruguay. Montevideo: *Sellow s.n.* (holotype, B not seen; isotype, MO!).

Urachne panicoides Trin. var. *brasiliensis* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 23. 1842. *Caryochloa montevidensis* Spreng. var. *brasiliensis* (Trin. & Rupr.) Döll ex Ekman, Ark. Bot. 13(10): 40. 1913. TYPE: "A Montevideo usque ad fines regni Paraguayani," *Sellow s.n.* (holotype, not located).

Piptochaetium tuberculatum E. Desv., in Gay, Fl. Chil. 6: 272. 1853. *Oryzopsis tuberculata* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 26. 1901. TYPE: Chile. Valdivia: *Gay s.n.* (holotype, P!).

Urachne depressa Steud., Syn. Pl. Glumac. 1: 123. 1854. TYPE: Chile. Rancagua: *Bertero 456* (holotype, P!).

Piptochaetium verrucosum Phil., Linnaea 33: 280. 1865. *Oryzopsis verruculosa* (Phil.) Speg., error for *verrucosa*, Anales Mus. Nac. Montevideo 4(2): 28. 1901. *Oryzopsis verrucosa* (Phil.) Speg., Revista Argent. Bot. 1(1): 12. 1925. TYPE: Chile. Valdivia: San Juan, *Philippi s.n.* (holotype, SGO 57334!; probable isotype, SGO 57350!).

Piptochaetium humile Phil., Anales Univ. Chile 93: 730. 1896. TYPE: Chile. Concon: médanos, *Philippi s.n.* (holotype, SGO 45087!).

Piptochaetium granulatum Phil., Anales Univ. Chile 93: 732. 1896. TYPE: Chile. Concon: *Philippi s.n.* (holotype, SGO 57333!).

Piptochaetium moelleri Phil., Anales Univ. Chile 93: 734. 1896. TYPE: Chile. Renaico, *Möller s.n.* (holotype, SGO 57332!).

Oryzopsis montevidensis (Spreng.) Speg. f. *trachycarpa* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Argentina. Misiones: Posadas, praderas de los alrededores, *Spegazzini s.n.* (holotype, LPS 13166!).

Oryzopsis montevidensis (Spreng.) Speg. f. *brasiliensis* Speg., Revista Argent. Bot. 1(1): 11. 1925. TYPE: Brazil. Rio Grande do Sul: Uruguayana, campos secos, *Spegazzini s.n.* (holotype, LPS 13175!).

Distribution. Found in Venezuela in the state of Trujillo, and widespread in southern South America in Bolivia, departments of La Paz and Cochabamba, central Chile, IV, VI, and VIII Regions, southern Paraguay, departments of Misiones and Paraguarí, southern Brazil, states of Paraná, Rio Grande do Sul, and Santa Catarina, southern Uruguay, departments of Colonia, Lavalleja, and Maldonado, and northern and central Argentina, provinces of Buenos Aires, Chaco, Córdoba, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. This species, which has been considered disjunct in Mexico, northern South America, and southern South America (Thomasson, 1980), has also been cited for Peru (Brako & Zarucchi, 1993) and southern Ecuador, province of Chinchipe (Jørgensen & León-Yánez, 1999). This distribution pattern makes it probable that it also occurs in Colombia, and, together with *P. panicoides*, would confirm one of the possible migration routes proposed by Thomasson (1980).

This species is the most frequent of the genus, growing on riversides, grasslands with rocky places and modified soils, up to 3700 m elevation.

Additional specimens examined. BRAZIL. **Paraná:** Ruta BR-280, hacia Horizonte, a 1 km de ruta BR-153, *Rúgolo et al. 1611* (MO). VENEZUELA. **Trujillo:** Carache, 220 m, *Rivero & Díaz 1384* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

24. Piptochaetium napostaense (Spegazzini) Hackel, Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 103. 1904. *Oryzopsis napostaensis* Speg., Anales Mus. Nac. Montevideo 4(2): 15. 1901. *Oryzopsis napostaensis* Speg. var. *macrophylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: alrededores de Carmen de Patagones, Feb. 1898, *C. L. Spegazzini 41 a* (lectotype, designated by Parodi (1944), LPS 2483!).

Oryzopsis napostaensis Speg. var. *brachyphylla* Speg., Anales Mus. Nac. Montevideo 4(2): 17. 1901. TYPE: Argentina. Buenos Aires: Sierra de Curamalal, Dec. 1899, *C. L. Spegazzini 41 b* (holotype, LPS 2469!).

Stipa capillifolia Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 95. 1904. TYPE: Argentina. Córdoba: Dep. Río I, pedanía, Villamonte, Ea. San Teodoro, *Stuckert 13803* (syntype, W not seen; isosyntypes, CORD!, LPS!), *Stuckert 14082* (syntype, not located).

Stipa hypogona Hack., Anales Mus. Nac. Buenos Aires 21: 73. 1911. TYPE: Argentina. Buenos Aires: Estación Tornquist, F.C.S., *M. Estrada s.n.*, Herb. *Stuckert 17397* (holotype, W not seen; isotype, US 3168626 not seen).

Distribution. Endemic to central Argentina in the provinces of Buenos Aires, Catamarca, Córdoba, La Pampa, Mendoza, Río Negro, and San Luis, up to 1900–2000 m elevation. This species grows in dry and arid grasslands and is a frequent species of the "caldenal," an open wild forest of "calden tree" (*Prosopis caldenia* Burkart), in the "Espinal" biogeographic province.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

25. Piptochaetium palustre Mujica-Sallés & Longhi-Wagner, Candollea 48: 15. 1993. TYPE: Brazil. Santa Catarina: Urupema, junto a la Estación Retransmisora del Morro de Campo Novo, 1680 m s.m., 25 Nov. 1984, *J. F. M. Valls et al. 8083* (holotype, ICN!; isotype, CEN!).

Distribution. Known only from southern Brazil at the type locality.

For a description and illustrations, see Cialdella and Arriaga (1998).

26. Piptochaetium panicoides (Lamarck) E. Desvaux, in Gay, Fl. Chil. 6: 270. 1853. *Stipa panicoides* Lam., Illustr. Genr. 1: 158. 1791. *Oryzopsis panicoides* (Lam.) Speg., Anales Mus. Nac. Montevideo 4(2): 31. 1901. TYPE: Uruguay. Montevideo: without locality, 1767, *Commerson s.n.* (isotypes, P!, MPU not seen, US not seen).

Oryzopsis setacea A. Rich., Dict. Hist. Nat. 12: 445. 1827. TYPE: Uruguay. Montevideo: *Commerson s.n.* (holotype, probably P not seen).

Piptochaetium setifolium J. Presl, Reliq. Haenk. 1: 222. 1830. *Stipa setifolia* (J. Presl) Kunth, Enum. Pl. 1: 182. 1833. *Urachne simplex* Trin. & Rupr. var. *peruviana* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 5: 23. 1842. *Oryzopsis setifolia* (J. Presl) Henrard, Meded. Rijks-Herb. 40: 57. 1921. TYPE: Peru. Sin localidad, *T. Haenke s.n.* (holotype, PR!).

Oryzopsis lejocarpa Speg., Anales Mus. Nac. Montevideo 4(2): 33. 1901. *Piptochaetium leiocarpum* (Speg.) Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, not located; isotype, LPS!).

Piptochaetium subnudum Phil., Anales Univ. Chile 93: 731. 1896. TYPE: Chile. Río Itata, *Philippi s.n.* (holotype, SGO not seen; isotypes, SGO 57374!, US not seen).

Piptochaetium leiocarpum (Speg.) Hack. f. *subpapillosa* Hack. ex Stuck., Anales Mus. Nac. Hist. Nat. Buenos Aires 13: 463. 1906. *Piptochaetium panicoides* (Lam.) E. Desv. f. *subpapillosum* (Hack. ex Stuck.) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 302. 1944. *Piptochaetium panicoides* (Lam.) E. Desv. var. *subpapillosum* (Hack. ex Stuck.) Petetin, in Correa, Fl. Patagónica, Colecc. Ci. Inst. Nac. Tecnol. Agropecu. 8(3): 339. 1978. TYPE: Argentina. Tucumán: without locality, *Lillo 4314* (holotype, not located; isotype, Herb. Arg. Stuckert 15418, CORD!).

Stipa lineolata Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 205. 1921. TYPE: Argentina. Tucumán: La Ciénaga, *Lorentz & Hieronymus 608* (holotype, B not seen).

Oryzopsis lejocarpa Speg. var. *major* Speg., Revista Argent. Bot. 1(1): 10. 1925. TYPE: Argentina. Jujuy: Sierra de Santa Bárbara, Sta. Cornelia, *Spegazzini 2490* (holotype, LPS 12641!).

Distribution. This species has a disjunct distribution within South America: an Andean area, including mountain regions of Venezuela, Colombia, and Peru (Brako & Zarucchi, 1993), widespread in Ecuador (Jørgensen & León-Yánez, 1999), Bolivia, Chile, and Argentina, in the provinces of Córdoba, Jujuy, Salta, and Tucumán, and a coastal zone limited to sandy soils of southern Brazil, Uruguay, and Argentina, in the provinces of Buenos Aires and Entre Ríos.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

27. Piptochaetium pilosum (Sánchez Vega) Cialdella & Giussani, stat. nov. Basionym: *Piptochaetium tovarii* Sánchez Vega subsp. *pilosa* Sánchez Vega, Arnaldoa 1(1): 29. 1991. TYPE: Peru. Cajamarca: entre Llacanora y Namora, 2750 m, *Sánchez Vega et al. 2459* (holotype, CPUN!; isotypes, MO!, USM!).

The florets of this species have lemmas with prickles, hooks, and macrohairs all over the surface, and a callus that is densely pubescent. These characters clearly distinguish *Piptochaetium pilosum* from *P. tovarii*, with florets without any epidermal appendage on the lemma and callus. These differences, together with the results of the cladistic analysis, make it reasonable to raise *Piptochaetium tovarii* subsp. *pilosa* to the rank of species.

Distribution. Peru in the departments of Cajamarca and Junín.

For a description and illustrations, see Cialdella and Arriaga (1998).

28. Piptochaetium pringlei (Beal) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 230. 1944. *Oryzopsis pringlei* Beal, Bot. Gaz. 15: 112. 1890. *Stipa pringlei* (Beal) Scribn., in Vasey, Contr. U.S. Natl. Herb. 3(1): 54. 1892. TYPE: Mexico. Chihuahua: dry ledges, Sierra Madre, 5 Nov. 1887, 8500 ft., *Pringle 1410* (holotype, US!; isotype, MO!). Figure 5D.

Plants perennial. *Culms* 0.5–1 m tall, terete, glabrous, pubescent below the nodes; nodes 2–3, reddish, compressed or enlarged, glabrous or slightly pubescent; internodes 7–20 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 6–18 cm long, scabrous, hispid to the base. *Ligules* 1–2.5 mm long, blunt or subacute, margins entire, hispid at the abaxial side. *Leaf blades* linear, flat, 10–30 cm long, 1–3 mm wide, glabrous, scabrous on the nerves and margins. *Peduncles* terete, slightly flattened, 30–50 cm long, longitudinally striate, hispid. *Inflorescences* 15–16 cm long, few-flowered (10 to 25 spikelets), with branches loosely disposed; pedicels flattened, up to 1 mm long, hispid. *Spikelets* fusiform, 9–12 mm long, 1.2–1.9 mm diam. *Glumes* subequal, longer than the floret, 9–12 mm long, acuminate, glabrous; lower glume 5- or 7-nerved; upper glume 7-nerved. *Floret* terete-fusiform, 7–10 mm long, 1–1.5(–1.9) mm diam. *Lemma* contracted below the crown, 7–10 mm long, smooth, shiny, with yellowish macrohairs, deciduous, and few prickles toward the crown; crown contracted at the base of the awn, inconspicuous, straight, not revolute, 0.4–0.8 mm diam., with rows of long macrohairs 0.8–1 mm long and prickles; callus 0.8–1 mm long, subacute, obliquely truncate, hairy, the upper hairs slightly longer than the callus; awn bigeniculate to almost straight, 1–2 (–3.5) cm long, persistent, hispid, scabrous toward the apex. *Palea* 6–7 mm long. Lodicules 2, ca. 1 mm long, acute. *Caryopsis* not seen.

Chromosome numbers. $2n = 42$ (Myers, 1947, as *Stipa pringlei* (Beal) Scribn.); $n = 21$ (Reeder, 1977, as *Stipa pringlei* (Beal) Scribn.).

Distribution. Southwestern United States and northern Mexico, up to 2000–2500 m elevation.

Additional specimens examined. U.S.A. **Arizona:** Cochise Co., 6 mi. up Carr Canyon, Huachuca Mountains, *Gould et al. 2456* (BAA, US); Williams, *Hitchcock 1903* (US); Mt. Lemmon, Santa Catalina Mts., near Tucson, *Soderstrom 141* (US). **California:** Santa Rita, *Silveus 3470* (TEX). **New Mexico:** Ranger Station, Queen, *Hitchcock 813* (BAA); Guadalupe Mountains, *Hitchcock 13553* (US). **Texas:** Black Mountains, *Tharp 4175* (TEX, US); Culberson Co., S McKittrick Canyon, top of Guadalupe Mts., *Warnock 12082* (TEX); Lincoln Co., *Hinckley & Hinckley 245* (TEX). MEXICO. **Coahuila:** Del Carmen Mts., *Marsh Jr. 629* (US). **Chihuahua:** Sierra Madre Occidental, Sierra Gazachic 35 km SW of Minaca, *Pennell 18929* (US); Sierra La Viga, 6 km E de Jame, Puerto Maravillas, *Villarreal et al. 1975* (XAL). **Sonora:** Morelos, El Rancho de Robles, *Vera Santos 1959* (MO, US); E of Cananea, Sierra de Los Ajos, *Beetle M-7856* (MO).

Piptochaetium pringlei is slightly similar to *P. fimbriatum* in that both species share the smooth surface of the lemma, only with macrohairs and few hooks near the crown. *Piptochaetium fimbriatum* differs in having a shorter floret, 3.5–5 mm long, and a blunt callus.

29. Piptochaetium ruprechtianum E. Desvaux, in Gay, Fl. Chil. 6: 274. 1853. *Oryzopsis ruprechtiana* (E. Desv.) Speg., Anales Mus. Nac. Montevideo 4(2): 12. 1901. *Stipa ruprechtiana* (E. Desv.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. TYPE: Brazil. Without locality, *Sellow s.n.* (holotype, LE-Trin not seen; isotype, US not seen; drawing of US isotype, *Herb. Parodi 4127* sheet b, BAA!).

Oryzopsis bicolor (Vahl) Speg. var. *major* Speg., Anales Mus. Nac. Montevideo 4(2): 9. 1901. TYPE: Argentina. Sierra de Tandil, *Spegazzini s.n.* (holotype, LPS 12515!; isotype, BAA!).

Distribution. Southern Brazil in the states of Rio Grande do Sul and Santa Catarina, Uruguay in the departments of Lavalleja, Maldonado, and Soriano, and Argentina in the provinces of Misiones and Buenos Aires. This species is frequent in rocky prairies, and in Brazil it grows in savannas.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

30. Piptochaetium sagasteguii Sánchez Vega, Arnaldoa 1(1): 17. 1991. TYPE: Peru. Cajamarca: Cerro El Guitarrero, ladera occidental del valle de Cajamarca, 2800 m, 15 Jan. 1983, *I. Sánchez Vega 2914* (holotype, CPUN!; isotypes, AAU not seen, CHAPA not seen, F not seen, HAO not seen, K not seen, MO!, US 3232467 not seen, USM not seen).

Distribution. Known from Peru in the departments of Cajamarca and La Libertad at elevations between 2700 and 3500 m.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

31. Piptochaetium seleri (Pilger) Henrard, Blumea 3: 452. 1940. *Oryzopsis seleri* Pilg., Verh. Bot. Vereins Prov. Brandenburg 51: 192. 1909. TYPE: Guatemala. Huehuetenango: between Todos los Santos and Chiantla, 3000 m, Sep.?, *Seler 3238* (holotype, B not seen; isotypes, BAA!, US 2767420 not seen). Figure 5F.

Plants perennial. *Culms* 20–90 cm tall, terete, glabrous; nodes 2 or 3, reddish, compressed, glabrous; internodes (4.5–)10–15 cm long. *Leaf sheaths* embracing the culms, generally shorter than the internodes, 8–9 cm long, glabrous. *Ligules* 0.8–2 mm long, blunt to subacute, membranous, margins entire, glabrous. *Leaf blades* linear, convolute, 5.5–12 cm long, 0.4–0.5 mm wide, abaxial side scabrous on the nerves, adaxial side glabrous. *Peduncles* terete, 22–26 cm long, longitudinally striate, glabrous. *Inflorescences* 7–22 cm long, few to many flowered (25 to 60 spikelets), with branches loosely disposed; pedicels angled, 0.4–1.5 cm long, glabrous. *Spikelets* fusiform, 4–5 mm long, 1–1.4 mm diam. *Glumes* subequal, longer than the floret, 4–5 mm long, shortly acuminate, 5-nerved, violaceous, hyaline toward the margin. *Floret* terete, slightly obovoid, 3–4.5 mm long, 1–1.2 mm diam. *Lemma* narrowed below the crown, 3–4.5 mm long, striate, with short macrohairs and hooks all over the surface; crown contracted at the base of the awn, straight, not revolute, 0.4–0.5 mm diam., with prickles and short macrohairs; callus 0.4–0.6 mm long, blunt, obliquely truncate, hairy, the hairs slightly longer than the callus; awn bigeniculate, 1–1.5 cm long, persistent, shortly hispid. *Palea* ca. 3.5 mm long. *Lodicules* 2, 0.8–1 mm long, acute. *Caryopsis* terete, slightly obovoid, 3–3.2 mm long, 0.8–0.9 mm diam.; hilum linear; embryo ¼ the length of the caryopsis.

Distribution. Widespread in Mexico and southern Guatemala, between 2000 and 3600 m.

Selected specimens examined. MEXICO. **Coahuila:** Cañón de San Lorenzo, Sierra de Zapalinamé, 3 km S of Saltillo, *Snow et al. 6721* (MO). **Distrito Federal:** Desierto de los Leones, *Lyonnet 2719* (US); lava fields ca. 2 km SSW of La Cima, R.R. station on either side of old hwy. 95, 14 Aug. 1960, *Iltis et al. 958* (US). **Hidalgo:** woodlands near Trinidad Iron Works, *Pringle 13249* (MO, US). **México:** Sierra de Las Cruces, *Pringle 5200* (MEXU, US); 10 km al E de Amecameca, sobre la carretera a Tlamacas, 13 Nov. 1977, *Rzedowski 35555* (MEXU); 27 km SW of Toluca on road to Temaxcaltepic, *Mick & Roe 180* (US); Llano Grande, *Matuda 19202* (MEXU); Llano Grande, near Río Río, *Sharp 44144* (US); Chapingo, Ixtapaluca, faldas del Cerro El Papayo, Campo Experimental Zoquiapán, *Zavala Ch. 245* (XAL); al SW del Centro Experimental Zoquiapán, *Velazco Torres & J. Trinidad s.n.* (XAL); Telapon, *Lyonnet & Elcoro 1948* (US); Parque Nacional Lagunas de Zempoala, *Traylor 61* (MEXU, US). **Michoacán:** Santa Clara del Cobre, Laguna de San Gregorio, *Escobedo 1478* (XAL); summit of Cerro San Andres, ca. 12 km N of Ciudad Hidalgo, *Beaman 4273*, *Beaman 4329* (US). **Morelos:** Zempoala, *Lyonnet 2511* (MEXU). **Oaxaca:** 18 mi. SW of city of Oaxaca, *Nelson 1373 a* (US). **Tlaxcala:** ca. 3 mi. NE of Tlaxco, *Sohns 604* (US). **Veracruz:** Acajete, *Rzedowski 11940* (MEXU); Calcahualco, end of passable portion of road from Coscomatepec-Escola-Jacal to Miguel Hidalgo and Tlachichuca, *Nee & Diggs 24775* (MO, XAL); La Joya, *Mejía S. 218* (XAL); Las Minas, vereda de Cruz Blanca a Rinconado, *Durán E. & Burgos 498* (XAL); Las Vigas, 1 km despues de pasar la presa del Alto Pixquiac rumbo a Tembladeras, *Chazaro & Robles 3792* (XAL); Manzanares, Las Vigas, *Ventura A. 18506* (XAL); Perote, Escobillo, *Sandoval 68* (XAL); Perote, por la brecha que va a Tonalaco en las faldas del Cofre de Perote, *Castillo et al. 1980* (XAL); Soledad Atzompa, *Martínez & Acosta P. 1063* (XAL); Xico, Tonalaquillo, *Arriaga C. 351* (XAL). GUATEMALA. **Huehuetenango:** Sierra de los Cuchumatanes, immediately N of Tojiah at km 322, on ruta nacional 9 N, *Beaman 3928* (US); near Tunimá, Sierra de los Cuchumatanes, *Steyermark 48274* (US); trail between Soloma and Santa Eulalia, Sierra de los Cuchumatanes, *Steyermark 48452* (US). **Totonicapán:** Desconsuelo, potrero natural, flora alpina, *de Koninck 114* (US); on the Tecum Uman Ridge at km 154 on ruta nacional nro. 1, ca. 20 km E of Totonicapán, *Beaman 4155* (US).

Beetle (1977) and Hitchcock (1951, under *Oryzopsis seleri*) placed *Piptochaetium seleri* in synonymy with *P. fimbriatum*. Both species have terete, slightly obovoid florets and lemma with macrohairs, but *P. fimbriatum* has smooth or thinly striate lemmas, without prickles or hooks, and a crown without epidermal appendages.

32. Piptochaetium setosum (Trinius) Arechavaleta, Anales Mus. Nac. Montevideo 1: 330. 1896. *Urachne setosa* Trin., Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 6(1): 124. 1834, nom illeg. superfl. TYPE: Chile. Without locality, *Cumming s.n.*, TRIN 1473.1 (lectotype, designated by Parodi (1944), LE not seen; isotype, US not seen).

Urachne fusca Nees ex Steud., Syn. Pl. Glumac. 1: 123. 1854. TYPE: Chile. Valparaíso: *Cumming 453* (isotype, K!).

Piptochaetium purpuratum Phil., Linnaea 29: 86. 1857. TYPE: "Chile. Valparaíso, Nov. 1854" (probable holotype, SGO 57419!).

Piptochaetium pallidum Phil. ex Griseb., Symb. Fl. Argent.: 279. 1879. TYPE: Chile. Cerro San Cristóbal, *Philippi s.n.* (lectotype, designated here, SGO 57412!).

Piptochaetium macrocarpum Phil., Anales Univ. Chile 93: 735. 1896. TYPE: Chile. Ñuble, *N. Briones s.n.* (holotype, SGO 45082!).

Distribution. This species presents, at the moment, a disjunct distribution in southern North America (California) and South America (Bark-

worth, 1986, 1993), where it grows in central Chile from Valparaíso to Valdivia.

Observation. This species has a strikingly prostrate habit in some specimens collected in California (Barkworth, pers. comm.).

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

Note. *Piptochaetium setosum* (Trin.) Arechav. was based on *Urachne setosa* Trin., a nomenclaturally superfluous name when published, as Trinius cited *Stipa panicoides* Lam. and *Oryzopsis setacea* A. Rich. as synonyms, both earlier published. Nevertheless, *P. setosum* is the correct name in *Piptochaetium* for *Urachne setosa* when *Stipa panicoides* and *Oryzopsis setacea* are considered synonyms of another species, *Piptochaetium panicoides* (Lam.) E. Desv.

33. Piptochaetium stipoides (Trinius & Ruprecht) Hackel, Anales Mus. Nac. Montevideo 1(4): 328. 1896.

33a. Piptochaetium stipoides (Trinius & Ruprecht) Hackel var. **stipoides.** *Urachne stipoides* Trin. & Rupr., Mém. Acad. Imp. Sci. St. Pétersbourg, sér. 6, Sci. Nat. 5: 25. 1842. *Oryzopsis stipoides* (Trin. & Rupr.) Speg., Anales Mus. Nac. Montevideo 4(2): 23. 1901. *Piptochaetium stipoides* (Trin. & Rupr.) Hack. var. *genuinum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 266. 1944, nom. inval. TYPE: Brazil. Brasilia meridionalis, *Sellow s.n.* (holotype, LE not seen).

Piptochaetium chaetophorum Griseb., Symb. Fl. Argent.: 298. 1879. *Piptochaetium ovatum* E. Desv. var. *chaetophorum* (Griseb.) Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 11: 104. 1904. TYPE: Argentina. Córdoba: Dpto. Punilla, Pan de Azúcar, *Hieronymus s.n., Herb. Grisebach 253* (holotype, GOET not seen; isotype, CORD!).

Piptochaetium cuspidatum Phil., Anales Univ. Chile 93: 732. 1896. TYPE: Chile. Salto de Conchalí, *Philippi s.n.* (holotype, SGO 57401!; isotype, US 1819510 not seen).

Piptochaetium ovatum E. Desv. var. *purpurascens* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 86. 1911. *Piptochaetium stipoides* (Trin. & Rupr.) Hack. var. *purpurascens* (Hack.) Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 272. 1944. TYPE: Argentina. Chaco: Dpto. 1 de Mayo, Margarita Belén, *Stuckert 19189* (lectotype, here designated, CORD!).

Piptochaetium ovatum E. Desv. f. *atrata* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 85. 1911. TYPE: Argentina. Chaco: Dpto. 1 de Mayo, Colonia Benítez, *Stuckert 18304* (holotype, W not seen; isotype, CORD!).

Stipa verruculosa Mez, Feddes Repert. Spec. Nov. Regni Veg. 17: 206. 1921. *Piptochaetium verruculosum* (Mez) Henrard, Meded. Rijks-Herb. 54: 380. 1927. *Piptochaetium verruculosum* (Mez) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940, comb. superfl. TYPE: Argentina. Buenos Aires: without locality, *Balansa s.n.* (holotype, B not seen; isotype, US not seen).

Piptochaetium grisebachi (Speg.) Herter, Revista Sudamer. Bot. 6(5–6): 141. 1940. *Oryzopsis grisebachi* Speg., Anales Mus. Nac. Montevideo 4(2): 4. 1901. TYPE: Argentina. Entre Ríos: Concepción del Uruguay, *Lorentz s.n.*, Flora Entrerriana 1691 (holotype, CORD!; isotype, LPS!).

Piptochaetium stipoides (Trin. & Rupr.) Hack. var. *parviflorum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 275. 1944. TYPE: Argentina. Buenos Aires: Pdo. Balcarce, Balcarce, *Martínez Crovetto 950 1/2* (holotype, BAA!).

Distribution. This variety presents, at the moment, a disjunct distribution (Thomasson, 1980; Barkworth, 1986, 1993) in the southwestern United States and Mexico (Beetle, 1977), and in South America, where it grows in southern Brazil in the states of Rio Grande do Sul and Santa Catarina. It is also widespread in Uruguay, in Canelones, Colonia, Flores, Florida, Lavalleja, Montevideo, Paysandú, Río Negro, Salto, Soriano, and Tacuarembó; in Chile, in VIII and IX Regions and in Región Metropolitana; and in Argentina in the provinces of Buenos Aires, Catamarca, Chaco, Córdoba, Corrientes, Entre Ríos, Jujuy, Misiones, Río Negro, and Santa Fe. This variety is known up to elevations of 2000 m in arid regions.

Additional specimens examined. ARGENTINA. **Chaco:** Margarita Belén, 1 Nov. 1908, *Stuckert 19208* (CORD). MEXICO. **Tamaulipas:** Sierra de San Carlos, Cerro de los Armadillos, 10 July 1930, *Bartlett 10225* (US).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

33b. Piptochaetium stipoides (Trinius & Ruprecht) Hackel var. **echinulatum** Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 271. 1944. TYPE: Argentina. Buenos Aires: Pdo. Puán, Villa Iris, *Parodi 13759* (holotype, BAA!).

The florets of this variety present the lemma with prickles partially covered by adjacent epidermal cells at the base (Cialdella & Arriaga, 1998: figs. 3D, 10J).

Distribution. This variety has been found in central Argentina in the provinces of Buenos Aires, La Pampa, and San Luis, and in northern Uruguay in the department of Salto.

For a description, illustrations, and specimens examined, see Cialdella and Arriaga (1998).

34. Piptochaetium tovarii Sánchez Vega, Arnaldoa 1(1): 25. 1991. TYPE: Peru. Cajamarca: Cajamarca, entre Cajamarca y Cumbemayo, Fundo Universidad, 3450 m, 22 May 1971, *I. Sánchez Vega & N. Vilhena 678* (holotype, CPUN!; isotypes, MO!, US 3232468 not seen).

Distribution. Southern Ecuador in the limited region between provinces of Loja and Azuay, and northwestern Peru in the departments of Piura, Cajamarca, and Ancash, at elevations between 2700 and 3450 m.

Additional specimens examined. ECUADOR. **Azuay-Loja:** Nudo de cordillera occidental y cordillera oriental, entre Oña y Rancho Ovejero, 1–2 Aug. 1959, *Barclay & Juajibioy 8455* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

35. Piptochaetium uruguense Grisebach, Symb. Fl. Argent.: 297. 1879. *Oryzopsis uruguayensis* (Griseb.) Speg., Anales Mus. Nac. Montevideo 4(2): 29. 1901. *Piptochaetium uruguense* Griseb. var. *genuinum* Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 290. 1944, nom. inval. TYPE: Argentina. Entre Ríos: Dpto. Uruguay, Concepción del Uruguay, 13 Nov. 1875, *P. G. Lorentz 471* (holotype, probably in GOET not seen; isotypes, BA!, CORD!).

Piptochaetium uruguense Griseb. var. *microcarpum* Parodi, Revista Mus. de La Plata, Secc. Bot. 6(25): 290. 1944. TYPE: Argentina. Corrientes: Dpto. San Martín, Yapeyú, *Parodi 12637* (holotype, BAA!).

Distribution and ecology. For the time being, this species presents a disjunct distribution in Mexico (Thomasson, 1980; Barkworth, 1986) and in South America, in Paraguay, departments of Misiones and Guairá, in western Uruguay, departments of Cerro Largo, Flores, Florida, Paysandú, and Rocha, and in northern and northeastern Argentina, provinces of Chaco, Corrientes, Entre Ríos, Misiones, Salta, and Santa Fe. *Piptochaetium uruguense* also grows in southern Brazil, state of Rio Grande do Sul, and it has been cited for Santa Catarina (Smith et al., 1982). This species grows in wet prairies.

Additional specimen examined. BRAZIL. **Rio Grande do Sul:** Fazenda Experimental de Criacao Bage, 1 Dec. 1945, *Swallen 7561* (MO).

For a description, illustrations, and other specimens examined, see Cialdella and Arriaga (1998).

36. Piptochaetium virescens (Kunth) Parodi, Revista Mus. La Plata, Secc. Bot. 6(25): 230. 1944. *Stipa virescens* Kunth, Nov. Gen. Sp. 1: 126. 1816. TYPE: Mexico. Guanajuato, Santa Rosa, Cuesta de Belgrado y La Buffa, *Humboldt & Bonpland s.n.* (holotype, P not seen; isotype, US 00141712 not seen). Figure 5C.

Stipa arsenii Hack., Repert. Spec. Nov. Regni Veg. 8: 515. 1910. *Piptochaetium virescens* (Kunth) Parodi var. *arsenii* (Hack.) Beetle, Phytologia 54: 4. 1983. TYPE: Mexico. Michoacán: Morelia, 2200 m, *Fr. Arsène 3211* (holotype, W not seen; isotypes, US not seen, MO 845899 not seen).

Plants perennial. *Culms* 0.70–1.30 m tall, terete, glabrous, occasionally hispidous below the nodes; nodes 3 or 4, brownish, compressed, glabrous; internodes 12–45 cm long. *Leaf sheaths* embracing the culms, shorter than the internodes, 9.5–15 cm long, glabrous. *Ligules* 1–2.5 mm long, blunt, margins entire, glabrous, sometimes hispidous at the abaxial side. *Leaf blades* linear, convolute, 10–35 cm long, 0.5–1 mm wide, longitudinally striate, glabrous, scabrous at the margins. *Peduncles* terete, 40–44 cm long, longitudinally ribbed, glabrous. *Inflorescences* 10–30 cm long, many-flowered (25 to 80 spikelets), with branches loosely disposed; pedicels slightly angled, 2–18 mm long, hispid. *Spikelets* fusiform, 6–8 mm long, 1.2–1.4 mm diam. *Glumes* subequal, longer than the floret, 6–8.5 mm long, shortly acuminate, 5-nerved, hyaline toward the margins. *Floret* terete-fusiform, 5.5–8(–9) mm long, 1 mm diam. *Lemma* slightly contracted below the crown, 5.5–8 mm long, thinly striate, with hooks and macrohairs uniformly disposed; crown contracted at the base of the awn, straight, not revolute, 0.5–0.7 mm diam., with prickles and rows of macrohairs 0.5–0.6 mm long, occasionally 1 mm long; callus 0.9–1 mm long, acute, occasionally subacute, densely hairy, the upper macrohairs slightly longer than the callus; awn bigeniculate, 13–20 mm long, persistent, hispid, scabrous toward the apex. *Palea* ca. 5 mm long. Lodicules 2, 1.4–1.6 mm long, acute. *Caryopsis* terete, 3–3.2 mm long, 0.9 mm diam.; hilum linear; embryo $\frac{1}{6}$ the length of the caryopsis.

Chromosome numbers. $2n$ = ca. 60 (Gould, 1966, as *Stipa virescens*).

Distribution. Guatemala and central and southern Mexico. This species was cited also for Venezuela, Barinas, in TROPICOS based on *J. Brunken & C. Perino 355* (MO), which we did not see.

Selected specimens examined. GUATEMALA. **Huehuetenango:** Cumbre Papal, between summit and La Libertad, *Steyermark 50955* (US). **Quezaltenango:** La Es-

peranza, *De Koninck 73 A and B* (US). **San Marcos:** Barrancos 6 mi. S and W of town of Tajumulco, NW slopes of Volcán Tajumulco, *Steyermark 36700* (US). MEXICO. **Chiapas:** SW of Mexican hwy. 190 near Rancho Nuevo, about 9 mi. SE of San Cristóbal las Casas, *Breedlove 14171* (US). **Distrito Federal:** Valle de Mexico, C. de Ajusco, *Matuda 25753* (MEXU); S. de Ajusco, *Pringle 6588* (MEXU, MO, US); Cerro Magdalena, Serranía de Ajusco, *Lyonnet 1877* (MO); 4 km W of San Andreas, Pedregal de San Angel, *Sohns 177* (US). **Hidalgo:** Tepeapulco, Cerro de Xihuingo, *Ventura A. 376* (MO); Tulancingo, open pine woods near reservoir at Tejocotal between Acaxochitlan and Puebla, *Moore Jr. 2843* (US); Real de Monte, *Matuda 18907* (US). **Jalisco:** 14–18 km SW of Tequila on Volcán de Tequila, *Breedlove 39241* (MO); Zapotlán, *Hitchcock 7169* (US); Sierra del Tigre, 3 mi. S of Mazamitla, *McVaugh 12268* (US); volcano of Colima, *Jones 479* (US). **México:** Valle de Mexico, C. Benacho, cerca de Amecameca, *Matuda 25724* (MEXU, MO); Ixtapaluca, 8 km S de Río Frío, *Koch 762* (MO); Popo Park, *Hitchcock 5965* (US); Cerro de Pinal, Otzoloapan, *Matuda et al. 31875* (US). **Michoacán:** in open pine forest and in open areas in and around the NE side of the Volcán de Paricutin, *Sohns 819* (MEXU); ca. 18 mi. S of Patzcuaron, *King & Soderstrom 5151* (MEXU); Las Cañas, *Rzedowski & McVaugh 623* (MO); Las Cañas, estribaciones inferiores noroccidentales del Cerro Patamban, Tangancicuaro, *Rzedowski & McVaugh 623* (US). **Morelos:** Sierra de Ajusco, *Pringle 6236* (MEXU, MO, US); Lagunas Zempoala, *Lyonnet 2498* (US). **Oaxaca:** 23 km de Tlaxiaco, rumbo a Chalcotongo, *Beetle M-4743* (MO); 0.5 km E de Las Huertas, Nundichi, Tlaxiaco, *Manzanero M. 450* (MO); 1 km al S de San Andrés, carr. Oaxaca–Puerto Angel, Miahuatlan, *Torres & Cedillo 875* (MO). **Puebla:** 8 ó 9 km al N de Tlaxco, al S de Cerro La Paila, *Chimal et al. 9* (MO); 5 mi. NE of Zacatepec, on hwy. 40 from Jalapa, *Soderstrom 493* (US); in pine forest, near crest of road pass, 46 mi. NW of Puebla on old hwy. to Mexico City, *Gould 10183* (US). **San Luis Potosí:** on the NE slopes of hills near Aguaje de García in the Sierra de Guadalcazar, *Sohns 1500* (US). **Tlaxcala:** Huamantla, 500 m al SW de Altamirano Guadalupe, *Guerrero et al. 632* (MO); 3 mi. NE of Tlaxco, *Sohns 601*, *Sohns 603* (US). **Veracruz:** Ayahualulco, *Nee 22928* (MO). **Zacatecas:** collected near Plateado, *Rose 2750* (US).

Piptochaetium virescens is similar to *P. indutum*: they share the floret and callus shape and the epidermal appendages on the lemma. *Piptochaetium indutum* can be recognized because it includes smaller plants, 15–35 cm tall, with smaller florets, (4–)5–6.25 mm long and 1 mm diam., with longer glumes, (7–)8–13.5 mm.

Piptochaetium virescens and *P. sagasteguii* are also related species, with similar floret characters; *P. sagasteguii* may be recognized because it includes smaller plants, 25–65 cm tall, with few-flowered inflorescences of 15 to 22 spikelets. The geographical distribution of these species is also different: *P. sagasteguii* is only known for Peru, while *P. virescens* can be found in Mexico and Guatemala.

Excluded Species from *Piptochaetium*

Piptochaetium mexicanum (Hitchc.) Beetle, Phytologia 54: 4. 1983 = *Nassella mexicana* (Hitchc.) Pohl, Taxon 39: 611. 1990. [Basionym: *Stipa mexicana* Hitchc., Contr. U.S. Natl. Herb. 24: 247. 1925.]

Nomina Nuda

Podopogon avenaceus Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. = *Piptochaetium avenaceum* (L.) Parodi.

Podopogon barbatus Raf. ex B. D. Jacks., Index Kew. 2: 580. 1894, nom. inval., as syn. of *Stipa avenacea* L. = *Piptochaetium avenaceum* (L.) Parodi.

Stipa diffusa Willd. ex Steud., Nomencl. Bot. (ed. 2) 2: 643. 1841, nom. inval., as syn. of *Stipa avenacea* L., non *Stipa diffusa* Walter (1788) = *Piptochaetium avenaceum* (L.) Parodi.

Avena stipoides Willd. ex Steud., Nomencl. Bot. (ed. 2): 2: 146. 1841, nom. inval., as syn. of *Milium mexicanum* Spreng. = *Piptochaetium fimbriatum* (Kunth) Hitchc.

Urachne panicoides Trin., in Martius, Fl. Bras. Enum. pl. 2(1): 376. 1829, Mém. Acad. Imp. Sci. St. Pétersbourg sér. 6, Sci. Nat. 3: 124. 1835, pro syn. nom. nud. = *Piptochaetium montevidense* (Spreng.) Parodi.

Piptatherum elegans P. Beauv., Essai Agrost.: 173. 1812, nom. nud. = *Piptochaetium panicoides* (Lam.) E. Desv.

Piptatherum panicoides Gilbert, Enum. Pl. Montev.: 117. 1873, nom. nud. = *Piptochaetium panicoides* (Lam.) E. Desv.

Piptatherum stipoides Gilbert, Enum. Plant. Montev.: 117. 1873, nom. nud. = *Piptochaetium stipoides* (Trin. & Rupr.) var. *stipoides*.

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Appendix 1

Examined material of *Piptochaetium*. Each specimen is cited by the last name of the first collector when there is more than one collector. Species number is indicated between parentheses.

1. *Piptochaetium alpinum* L. B. Smith
2. *Piptochaetium angolense* Philippi
3. *Piptochaetium angustifolium* (Hitchcock) Valencia & Costas
4. *Piptochaetium avenaceum* (L.) Parodi
5. *Piptochaetium avenacioides* (Nash) Valencia & Costas
6. *Piptochaetium bicolor* (Vahl) E. Desvaux
7. *Piptochaetium brachyspermum* (Spegazzini) Parodi
8. *Piptochaetium brevicalyx* (E. Fournier) Ricker
9. *Piptochaetium burkartianum* Parodi
10. *Piptochaetium cabrerae* Parodi
11. *Piptochaetium calvescens* Parodi
12. *Piptochaetium confusum* Parodi
13. *Piptochaetium cucullatum* Rosengurtt & Izaguirre de Arturio
14. *Piptochaetium featherstonei* (Hitchcock) Tovar
15. *Piptochaetium fimbriatum* (Kunth) Hitchcock
16. *Piptochaetium hackelii* (Arechavaleta) Parodi
17. *Piptochaetium hirtum* Philippi
18. *Piptochaetium indutum* Parodi
19. *Piptochaetium jubatum* Henrard
20. *Piptochaetium lasianthum* Grisebach
21. *Piptochaetium lejopodum* (Spegazzini) Henrard
22. *Piptochaetium medium* (Spegazzini) Torres
23. *Piptochaetium montevidense* (Sprengel) Parodi
24. *Piptochaetium napostaense* (Spegazzini) Hackel
25. *Piptochaetium palustre* Mujica-Sallés & Longhi-Wagner
26. *Piptochaetium panicoides* (Lamarck) E. Desvaux

27. *Piptochaetium pilosum* (Sánchez Vega) Cialdella & Giussani
28. *Piptochaetium pringlei* (Beal) Parodi
29. *Piptochaetium ruprechtianum* E. Desvaux
30. *Piptochaetium sagasteguii* Sánchez Vega
31. *Piptochaetium seleri* (Pilger) Henrard
32. *Piptochaetium setosum* (Trinius) Arechavaleta
33. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel
33a. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel var. *stipoides*
33b. *Piptochaetium stipoides* (Trinius & Ruprecht) Hackel var. *echinulatum* Parodi
34. *Piptochaetium tovarii* Sánchez Vega
35. *Piptochaetium uruguense* Grisebach
36. *Piptochaetium virescens* (Kunth) Parodi

Aleman 267 (26); Alonso J. 151 (20); Andrews s.n. (4); Arriaga C. 351 (31); Arzivenco 349 (20), 352 (28).

Baker 115 (5), 1155 (5); Banda 132 (8); Barclay 8455 (34); Barkley 14 A 660 (15); Bartlett 10225 (33a); Bartley 2011 (4); Beaman 3928 (31), 4155 (31), 4273 (31), 4329 (31), 4387 (36); Beetle M-141 (36), M-4743 (36), M-7086 (36), M-7338 (15), M-7742 (15), M-7856 (28), M-7864 (15); Berkley 1579 (4); Biswell 94408 (4); Boechat 160 (28), 161 (20); Bonner 354 (4); Boott s.n. (4); Boufford 18242 (4); Bozeman 8842 (4); Brandegee 31 (15), 34 (15); Brant 2239 (15); Braun 1422 (4), 942 (4); Breedlove 14171 (36), 39241 (36), 43293 (15), 44133 (15); Bro. Arsène 2699 (36), 5305 (36), 5375 (36), 6749 (36); Brunken 234 (15), 247 (36), 387 (36); Burgess 227 (4).

Calzada 4645 (15); Carter 2396 (15); Castillo 1980 (31); Chapman 1037 (4); Chase 7220 (4), 7312 (4), 7401 (4); Chazaro 3792 (31); Chiang 9077 (15); Chimal 9 (36), 1954 (31); Churchill 123 (4), s.n. (4); Cole s.n. (4); Collins s.n. (4); Combo 876 (4); Commons 269 (4); Correll 353 (4), 13699 (15), 16170 (4); Cronquist 4311 (4), 4432 (4), 5014 (4), 5075 (4); Curtiss 5834 (5).

Darrow 1287 (15); Davidse 9287 (15), 9485 (15), 9832 (36), 10031 (15), 11137 A (33a), 29775 (15); De Chalmot s.n. (4); De Koninck 73 (36), 114 (31); Deam 20709 (4), 36302 (4), 40704 (4), 64413 (4); Demaree 14586 (4), 19003 (4), 63483 (4); Dowell 7309 (5); Duncan 9485 (4); Durán E. 498 (31).

Earle 165 (15); Early s.n. (4); Eggert 36 (4), s.n. (4); Egler 41–136 (4); Ellis 1113 (31); Escobedo 1478 (31).

Faircloth 5079 (4), 5798 (4), 7070 (4); Felger 92–794 (15); Fernald 7760 (4); Fernández 734 (28), 735 (20); Ferris 2736 (15), 2812 (15); Fisher 108 (31), s.n. (31), s.n. (4); Fogg Jr. 2224 (4); Fredholm 5092 (5), 5725 (5); Freeman 54117 (4).

Garber s.n. (4); Gentry 8492 (15); Gleason 8537 (4); Godfrey 3686 (4), 8085 (4), 67795 (4); Gould 2456 (28), 3768 (28), 4419 (15), 9211 (8), 9602 (15), 9661 (15), 10183 (36), 15409 (4); Griffiths 94 (15), 107 (28), 4836 (28), 4976 (28), 7032 (15); Griscom 16409 (4); Guerrero 632 (36); Gutte 185 (36).

Hall 764 (4); Harkins 809 (4); Harvey 1038 (3), 1458 (15), 1764 (4), 1854 (4); Havard 26 (15), s.n. (15); Henderson 91–03 (4), 94–29 (4); Henrickson 15143 a (15), 15226 (15); Hermann 3201 (4), 4198 (4); Hernandez Xolocotzi X-2443 (15), X-2828 (36), X-2836 (36); Hill 14632 (15); Hinckley 245 (28), 493 (28); Hinton 1336 (36), 1893 (36), 2315 (36), 2316 (36); Hitchcock 520 (4), 812 (5), 813 (28), 837 (15), 967 (5), 1271 (4), 1318 (4), 1341 (4), 1346 (4), 1903 (28), 3715 (15), 3776 (15), 5947 (36), 5965 (36), 5973 (36), 6019 (36), 6266 (36), 6733 (8), 7151 (36), 7169 (36), 7677 (28), 7681 (28), 7741 (15), 12616 (4), 13511 (15), 13553 (28), s.n. (4); Hoffmann s.n. (4); Hoge 260 (15); Hoogstraal 991 (36); House 2101 (4).

Iltis 213 (15), 214 (8), 958 (31), 23032 (4); Innes 1130 (15).

Jacob 815 (4); Jones 479 (36), 24157 (4).

Kearney 10114 (15), 10541 (28); Kearney Jr. 1102 (4); Kellogg 82 (4); King 3378 (31), 5132 (36), 5151 (36); Kneucker 564 (4); Knieskern s.n. (4); Koch 762 (36), 75709 (36), 77110 (15); Kral 2065 (4), 25586 (15), 34987 (4), 42587 (4), 45353 (4), 45934 (4), 46012 (4), 46479 (4), 55030 (4); Krauch 6495 (15).

Larrick 249 (4); Latham 2755 (4), 4087 (4), 22391 (4); Le Doux 2086 (31); Le Sueur 143 (15); Leavenworth 1077 (36); Lemmon 2923 (15), 4678 (28); Liberman 1110 (26); Longhi-Wagner 2121 (1), 2497 (1); Lundell 13153 (15); Luz 39 (26), Lyonnet 48 (15), 62 a (36), 1826 (36), 1877 (36), 1948 (31), 2498 (36), 2511 (31), 2512 (31), 2527 (36), 2684 (36), 2719 (31).

Mackenzie 3109 (4); Madrigal A. s.n. (15); Manzanero M. 450 (36); Marsh Jr. 629 (28); Martínez 1063 (31); Matthews s.n. (4); Matuda 18907 (36), 19202 (31), 21268 (36), 21645 (36), 25724 (36), 25753 (36), 25755 (36), 25777 (36), 29473 (36), 29776 (3), 31875 (36); McCarthy s.n. (4); McDaniel 1811 (4); McDougall 1818 (4); McGregor 57 (15), 406 (15); McVaugh 12268 (36); Mearns 2573 (28); Meislahn 191 (5); Mejía S. 218 (31); Mendoza 2640 (15); Metcalfe 746 (15); Metzler 2 (36); Mez 3164 (15), 3166 (15); Mick 87 (8), 180 (31), 287 (15), 305 (36); Miller Jr. s.n. (4); Mohr s.n. (4); Moore 3172 (15), 3605 (15), 4164 (15); Moore Jr. 1233 (31), 2843 (36), 5583 (36); Moorgen s.n. (29); Morong s.n. (4); Mueller 2342 (15), 2442 (15), 7948 a (15); Mujica Sallés 2 (20), 22 (28), 42 (26), 46 (26), 47 (26), 63 (33 a), 72 (26), 74 A (26), 81 (20), 83 (29), 130 (35), 141 (22), 142 (22), 144 (35), 151 (20), 155 (22), 166 (26).

Nealley s.n. (4); Neally 129 (15); Nee 22928 (36), 24775 (31); Nelson 1373 (36), 1373a (31); Noyes s.n. (4).

O'Neill 491 (4); Ortiz 1132 (36), 1194 (36).

Palmer 339 (15), 5154 (4), 5248 (4), 24541 (4), 31887 (15); Pedersen 5188 (35), 13333 (24); Peebles 3389 (15); Pennell 17704 (15), 8929 (28), 18940 (15); Peterson 4010 (15); Piedmont 4311 (4); Plank 53 (4); Pringle 18 (28), 502 (15), 639 (15), 3035 (15), 4759 (36), 5200 (31), 6236 (36), 6588 (36), 7606 (8), 8595 (15), 9574 (36), 13249 (31), s.n. (15); Purpus 3589 (15).

Quarín 3163 (33a).

Redfield 4317 (4); Reeder 233 (4), 2221 (31), 3295 (15); Renvoize 3025 (20), 4143 (23); Reverchon 4128 (4), s.n. (4); Rivero 1384 (23); Robinson 1 (4); Rodriguez 1284 (31); Roivainen 481 (11); Rolfe 43 (4); Rose 2750 (36), 5671 (36), 8680 (8), 8700 (36), 8744 (15); Rugel 1849 (4), s.n. (4); Rúgolo 1611 (23); Ruiz 326 (15); Ruth 93 (4), s.n. (4); Rzedowski 623 (36), 11940 (31), 16904 (15), 17547 (15), 17704 (15), 35555 (31), 35863 (8), 50768 (8).

Sánchez Vega 2458 (34), 2769 (34), 2935 (30), 4984 (30); Sánchez-Ken 141 (15); Sandoval 68 (31); Schaack 2881 (4); Schinini 19229 (35); Schultz 41 (4), 14705 (23); Scribner 138 (4), 266 (4); Scully 652 (4); Serrato Sánchez s.n. (15); Seymour 109 (4), 1060 (4); Sharp 44144 (31), s.n. (4); Shinners 7029 (4); Shreve 7707 (15); Silveus 727 (15), 785 (15), 3470 (28); Simpson s.n. (4); Smith 926 (36), 3327 (18), 8302 (14), 10109 B (18), 10331 (26), 10488 (18), 10960 (34), 10964 (18), 11038 (18), 11794 A (18); Snow 6721 (31); Soderstrom 141 (28), 493 (36), 752 (15); Sohns 177 (36), 289 (15), 300 (15), 424 (15), 505 (15), 507 (15), 533 (15), 534 (15), 538 (36), 553 (8),

581 (15), 601 (36), 603 (36), 604 (31), 782 (15), 790 (36), 799 (36), 804 (36), 819 (36), 977 (36), 982 (36), 1012 (31), 1016 (31), 1022 (15), 1064 (15), 1147 (15), 1500 (36), 1535 (8); Solomon 1535 (4), 1710 (4), 11342 (23); Sperry 370 (15); St. Pierre 888 (36); Standley 40512 (15), 40699 (15), s.n. (15); Stanford 2482 (4), 2604 (15); Steyermark 3172 (15), 36700 (36), 48274 (31), 48452 (31), 50955 (36); Strong 1342 (4); Svenson 10246 (4); Swallen 951 (4), 1109 (15), 7561 (35).

Talbot 8 (4); Taylor 276 (15), 6254 (15); Tenorio 1197 (15); Tharp 4175 (28); Thieret 19497 (4), 22502 (4), 28558 (4); Thorne 2592 (4), 3348 (4); Toolin 2222 (15); Torres 875 (36), 1226 (29); Tracy 130 (28), 4544 (4), 7031 (5), s.n. (4); Traylor 61 (31); Tuckerman 848 (4).

Valencia 442 (22), s.n. (23); Valls 1233 (20), 2215 (20), 2805 (20), 2821 (33 a), 2931 (20), 2939 (33 a), 12188 (22), 12259 (35); Van Eseltime 127 (4); Van Schaack 3575 (4); Van Sickle s.n. (4); Vasey s.n. (4); Velazco Torres s.n. (31); Ventura A. 376 (36), 2153 (15), 18506 (31); Vera Santos 24 (15), 1921 (15), 1922 (28), 1959 (28), 2155 (15); Villarreal 1975 (28).

Warner s.n. (4); Warnock 12082 (28), 46717 (15); Warnock T 598 (15); Waterfall 6322 (15), 12627 (15), 14854 (4), 16410 (36); Weatherby 4122 (4), 5831 (4), 6234 (4); Weatherways 16 (4), 37 (4); West 26673 (4); Whiting 811 (15), 887 (15); Wilcox s.n. (15); Wolff 4974 (4); Wooton s.n. (15); Wynd 643 (15).

Yacolucci 843 (4).

Zanin s.n. (1), 18 (1); Zavala Ch. 245 (31), 862 (15); Zöllner 8672 (32).

Appendix 2

Specimens of *Hesperostipa* and *Nassella* used for morphological and cladistic analyses, as outgroups of *Piptochaetium.*

Hesperostipa comata (Trinius & Ruprecht) Barkworth (= *Stipa comata* Trin. & Rupr.).

U.S.A. **Colorado:** El Paso Co., *Ehlers 7526* (UTC). **Nevada:** Elko Co., E side of Ruby Mtns., 0.7 road mi. S of Shantytown, *Williams et al. 84–49–8* (UTC). **Utah:** Garfield Co., located at the head of South Fork, Dugout Creek on the North Mountain in the Henry Mountains, *Nelson s.n.* (UTC 101953).

Hesperostipa neomexicana (Thurber) Barkworth (= *Stipa pennata* L. var. *neomexicana* Thurber).

U.S.A. **Arizona:** without locality, *Williams 3051* (BAA). **Texas:** San Antonio, *Silveus 1215* (BAA).

Hesperostipa spartea (Trinius) Barkworth (= *Stipa spartea* Trin.).

U.S.A. **Colorado:** Bookvale, Clear Creek Co., *Churchill s.n.* (BAA 15155). **Illinois:** Stark Co., Wady Petra, *Chase 808* (BAA). **Indiana:** Pulaski Co., sandy soil along Pennsylvania railroad and hwy. 29, 2.3 mi. S of Winamac, *Potzger 4243* (BAA).

Nassella charruana (Arechavaleta) Barkworth (= *Stipa charruana* Arechav.).

ARGENTINA. **Entre Ríos:** Gualeguaychú, *Burkart 25865* (SI); Gualeguaychú, ruta 12, km 180, *Burkart & Crespo 22895* (SI).

Nassella leucotricha (Trinius & Ruprecht) R. W. Pohl (= *Stipa leucotricha* Trin. & Rupr.).

MEXICO. **Coahuila:** Arteaga, Sierra de Arteaga, cañón de Jame, 5 mi. E de Jame, *Hoge 249* (UTC). U.S.A. **California:** Sonoma Co., near Sonoma, *Heller 5350* (SI). **Texas:** Bee Co., *Herb. Univ. Texas 2154* (SI); Karnes Co., roadside shoulder immediately S of Karnes City, *Isely 10634* (UTC).

Nassella meyeniana (Trinius & Ruprecht) Parodi (= *Urachne meyeniana* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Cochinoca, Abra Pampa, *Venturi 9385* (SI). **Humahuaca:** Tres Cruces, *Parodi 9609* (SI); Sierra del Aguila, *Venturi 8726* (SI).

Nassella pubiflora (Trinius & Ruprecht) E. Desvaux (= *Urachne pubiflora* Trin. & Rupr.).

ARGENTINA. **Jujuy:** Humahuaca, camino a Palca de Aparzo, *Kiesling & López 3624* (SI). **Tucumán:** Tafí, km 82, Quebrada del Barón, *Diers 282* (SI).

Nassella pulchra (Hitchcock) Barkworth (= *Stipa pulchra* Hitchc.).

U.S.A. **California:** Marin Co., 5 mi. W of Mill Valley, *Beetle 2722* (SI); Contra Costa Co., Orinda, in sandy soil of open cut, *Beetle 1718* (SI); Marin Co., San Rafael Hills, *Howell 16251* (UTC).

Nassella pungens E. Desvaux

CHILE. **IV Región:** Coquimbo, *Yiles 472* (SI).

Nassella tenuissima (Trinius) Barkworth (= *Stipa tenuissima* Trin.).

MEXICO. **Veracruz:** between Tziutlán and Perote, *Beetle M-581* (UTC). ARGENTINA. **Córdoba:** Ea. San Teodoro, *Stuckert 198* (SI). **La Pampa:** Toay, Ea. Anquiló, *Rúgolo 1060* (SI). **Tucumán:** Tafí del Valle, *Hueck 9* (SI).

Nassella trichotoma (Nees) Hackel ex Arechavaleta (= *Stipa trichotoma* Nees).

ARGENTINA. **Buenos Aires:** Bolívar, Pirovano, *Burkart 7076* (SI); Tandil, *Troncoso 1290* (SI). **Entre Ríos:** F. Carbó, orillas de vías férreas, *Burkart 18129* (SI).

Appendix 3

List of characters and character states. A description of the characters and character states and their range of variation are presented as considered in the cladistic analysis.

1. Lemma margins: not involute = 0; involute = 1.
2. Palea shape: flat on abaxial surface = 0; bikeeled on the abaxial surface = 1.
3. Palea length: half the length of the lemma to equal the length of the lemma = 0; longer than the lemma = 1; shorter than half the length of the lemma = 2 (Fig. 2A, B).
4. Palea venation: nerveless = 0; 2-nerved = 1.
5. Long fundamental cells of the lemma epidermis: absent = 0; present = 1.
6. Fundamental cell sidewalls: irregularly sinuate = 0; regularly dentate = 1; regularly sinuate = 2. Epidermal characters (5, 6), were taken from Thomasson (1978a), Barkworth (1990), and Torres (1997).
7. Callus length: shorter than 0.8 mm = 0; equal to or longer than 0.8 mm = 1. Callus length is variable within *Piptochaetium*; it is usually long in species with cylindrical or obconical florets but short in obovoid or lens-shaped florets. In *Nassella* the callus is variable in length, while it is always long in *Hesperostipa.*
8. Callus shape: acute or subacute = 0 (Fig. 5A–E); blunt or truncate = 1 (Fig. 5F–H). The callus, when short, is generally truncate or blunt; if long, it is acute or subacute. Callus shape varies also within *Nassella* s.l., while in *Hesperostipa* it is always acute. Charac-

ters 7 and 8 were traditionally considered as diagnostic to identify *Piptochaetium* sects. *Podopogon* and *Piptochaetium* (Parodi, 1944; Sánchez Vega, 1991; Cialdella & Arriaga, 1998). *Piptochaetium* sect. *Podopogon* generally included species with a long and acute or subacute callus, while *Piptochaetium* sect. *Piptochaetium* presented species with a short and blunt callus.

9. Callus pubescence: glabrous or slightly hairy = 0; densely hairy = 1. Most *Piptochaetium* species have florets with a densely pubescent callus (Fig. 5A–G). It is usually glabrous or only slightly pubescent in *Piptochaetium brevicalyx* (Fig. 5H), *P. calvescens*, *P. cucullatum*, *P. hirtum*, *P. lejopodum*, *P. montevidense*, *P. panicoides*, and *P. tovarii*. In *Nassella* the callus is glabrous or pubescent, with trichomes densely to slightly disposed, while in *Hesperostipa* the callus is always densely pubescent.
10. Awn: persistent = 0; deciduous = 1.
11. Inflorescence branches: densely flowered = 0; not densely flowered = 1. This character varies among species of *Piptochaetium* and *Nassella*, in which the branches may be densely or loosely flowered, while in *Hesperostipa* branches are loosely flowered.
12. Upper glume length: longer than the floret = 0; equal to the floret = 1. Species of *Piptochaetium*, *Nassella*, and *Hesperostipa* have upper glumes longer than the floret. Only in *P. alpinum* and *P. brevicalyx* is the upper glume as long as the floret.
13. Floret shape: terete to fusiform = 0 (Fig. 5A–G); obconical = 1 (Cialdella & Arriaga, 1998, fig. 8B, D); obovoid to globose = 2 (Fig. 5H); lens-shaped = 3 (Cialdella & Arriaga, 1998: fig. 10C, D). Floret shape varies among species of *Piptochaetium*, being terete, fusiform, obconical, obovoid, or lens-shaped. *Nassella* presents terete, obovoid, or lens-shaped florets, while in *Hesperostipa* florets are always terete.
14. Lateral compression of the floret: absent or slightly compressed = 0 (Fig. 5A–H); conspicuously compressed = 1 (Cialdella & Arriaga, 1998: figs. 9C, 10C, D). This character is variable among species of *Piptochaetium* and *Nassella*, while in *Hesperostipa* the florets are never laterally compressed.
15. Lemma pubescence: absent = 0 (Figs. 1A, 5H); present = 1 (Figs. 1B, 5G).
16. Papillae of the lemma: absent = 0; present = 1 (Cialdella & Arriaga, 1998: figs. 2D, 10C). Papillae are found in a few species within *Piptochaetium* and *Nassella*, but are always absent in *Hesperostipa*.
17. Prickles of the lemma: absent = 0; present = 1 (Fig. 1C, D).
18. Prickles over almost all the lemma surface: absent = 0; present = 1 (Fig. 2D).
19. Prickles on the distal third of the lemma: absent = 0; present = 1 (Figs. 2C, 5A, B). Hooks are similar to prickles, although these appendages differ slightly (Ellis, 1979). These characters were recognized as homologous by Metcalfe (1960). Intermediate forms can also be found, making it a difficult character to classify. In addition, the presence and distribution of hooks and prickles are similar in all the species analyzed. These epidermal appendages are found in some species of *Piptochaetium*, *Nassella*, and all species of *Hesperostipa*. Distribution of prickles (characters 18, 19) varies among species, although it is always constant within species. Only the distribution of appendages in *P. stipoides* var. *stipoides* (Cialdella & Arriaga, 1998: fig. 10F–I) is highly variable, even within a specimen.
20. Base of prickles: surrounded but not covered by adjacent epidermal cells = 0; partially covered by adjacent epidermal cells = 1 (Cialdella & Arriaga, 1998: fig. 3D). Partially covered prickle bases occur only in *Piptochaetium stipoides* var. *echinulatum* Parodi.
21. Lemma width just below the crown: as wide as the crown = 0; narrower than the crown = 1. This character is related to floret shape: lemmas of cylindrical florets are usually as wide as the crown or slightly narrowed, while in obconical, obovoid, and lens-shaped florets lemmas are conspicuously narrowed below the crown, being more conspicuous in gibbous florets.
22. Crown contracted to the base of the awn: absent = 0; present = 1 (Fig. 5). The crown concept was discussed by different authors (Spegazzini, 1901; Parodi, 1944; Barkworth, 1990; Muñoz-Schick, 1990; Jacobs et al., 1995; Cialdella & Arriaga, 1998). As interpreted here, it refers to the distal portion of the lemma, which is fused to the base of the awn (Barkworth, 1990; Cialdella & Arriaga, 1998). In *Piptochaetium* the crown can be contracted or not; when not contracted, it exceeds the diameter of the awn (Cialdella & Arriaga, 1998: figs. 9E, 10B). *Nassella* and *Hesperostipa* present a contracted crown, being membranous, loose, parted, and, in some species of *Nassella*, sheathing at the base of the awn (Barkworth, 1990).
23. Crown shape: straight, not revolute = 0 (Cialdella & Arriaga, 1998: fig. 10E); revolute toward the outside = 1 (Cialdella & Arriaga, 1998: fig. 9E). Some species of *Piptochaetium* show a revolute crown like a ring, generally covered by prickles, hooks, and sometimes macrohairs. In *Nassella* and *Hesperostipa* the crown is always straight.
24. Macrohairs in the crown: absent = 0 (Fig. 2A); present = 1 (Fig. 2C). This character is only variable in *P. stipoides* var. *stipoides* and *P. fimbriatum*. These appendages are frequently associated with other types of epidermal appendages such as prickles and hooks.
25. Papillae in the crown: absent = 0; present = 1 (Cialdella & Arriaga, 1998: fig. 3C). These appendages are found in a few species of *Piptochaetium*, while they are absent in *Nassella* and *Hesperostipa*.
26. Prickles in the crown: absent = 0 (Fig. 2A); present = 1 (Fig. 2C, D). This type of epidermal appendage is frequent in several species of *Piptochaetium* and *Nassella*, and completely absent in a few species; in *Hesperostipa* it is always present.
27. Awn shape: thread-like = 0 (Fig. 5H); cone-shaped = 1 (Cialdella & Arriaga, 1998: fig. 9F). In *Nassella*, *Hesperostipa*, and almost all species of *Piptochaetium*, the awn is thread-like, bigeniculate, shortly hispid, and twisted in its basal portion. Only in *Piptochaetium cucullatum* is the awn cone-shaped, right or slightly curved but not twisted, its base as wide as the crown (0.9–1 mm wide).
28. Floret length/width ratio: > 3.6 = 0; < 3.5 = 1.
29. Crown width: narrow [0.4–0.6(–0.9) mm diam.] = 0; wide (1–1.8 mm diam.) = 1. In *Piptochaetium*, the crown is narrow when contracted to the base of the awn, except in *Piptochaetium cucullatum*, which presents a wide and contracted crown (Cialdella & Arriaga, 1998: fig. 9F) due to the conical shape of the awn. In *Nassella* and *Hesperostipa* the crown is always narrow in shape.

SYSTEMATIC REVISION AND PHYLOGENY OF *PASPALUM* SUBGENUS *CERESIA* (POACEAE: PANICOIDEAE: PANICEAE)[1]

Silvia S. Denham, Fernando O. Zuloaga, and Osvaldo Morrone[2]

Abstract

Twenty-five species are treated in this work, in which exomorphological characters are analyzed cladistically. Species of *Paspalum* subg. *Ceresia* are characterized by their rigid, filiform to lanceolate blades, inflorescences with one to several racemes, rachis of the racemes winged and hyaline to membranous, spikelets pilose, occasionally glabrous, with the upper anthecium pale, hyaline to membranous, occasionally chartaceous, and the upper lemma not enclosing the tip of the upper palea. Species grow in South America from Mexico to Argentina and Uruguay. A cladistic analysis of subgenus *Ceresia* was conducted to test its monophyly, and to establish its relationship with other groups of *Paspalum*. A key to the species in subgenus *Ceresia* is given, as well as morphological description and illustration, and distribution maps.

Key words: America, *Ceresia*, cladistics, *Paspalum*, Poaceae.

Paspalum L. includes approximately 330 species distributed in tropical and subtropical regions of America, with a few taxa growing in the Old World (Clayton & Renvoize, 1986). Due to its large number of species, and the morphological variation present within the genus, *Paspalum* has been divided into subgenera, sections, or informal groups mainly on the basis of morphological characters, such as inflorescence type or features of the spikelet (Nees, 1829; Doell, 1877; Chase, 1927; Pilger, 1929; Clayton & Renvoize, 1986; Morrone et al., 1995, 1996, 2000; Cialdella et al., 1995).

Chase (1929) divided *Paspalum* into subgenera *Paspalum* and *Ceresia* (Pers.) Rchb., characterizing the latter by its foliaceous rachis, with one to several racemes per inflorescence and spikelets densely pilose, with long white hairs, mainly along the margins of the upper glume and lower lemma.

Taxonomic studies in *Ceresia* are fragmentary; with respect to the subgenus, these *Paspalum* species have been analyzed in regional works or floral treatments (Nash, 1912; Chase 1927, 1929; Pilger, 1929; Hitchcock, 1951; Burkart, 1969; Rosengurtt et al., 1970; Sendulsky & Burman, 1978, 1980; da Silva et al., 1979; Pohl, 1980; Judziewicz, 1990; Renvoize, 1998; Rodríguez, 1998).

The present taxonomic treatment revises *Paspalum* subg. *Ceresia*, considering vegetative and reproductive characters, analyzing habitat and distribution range. A cladistic analysis was further performed in order to test the monophyly of the subgenus and to establish the relationships of its species.

History

Ceresia was established at the generic level by Persoon (1805–1807), on the basis of *C. elegans* (= *Paspalum membranaceum* Lam., non Walt., 1788). Subsequently, Reichenbach treated *Ceresia* as a subgenus of *Paspalum* (Chase, 1929). Several species were described in *Ceresia* in the 19th century (Flüggé, 1810; Trinius, 1826, 1828–1836, 1834; Nees, 1829; Doell, 1877).

Nees (1829) considered, within *Paspalum*, section *Digitaria*, including *P. pectinatum* and species currently treated in *Axonopus*; section *Lanigeri*, including *P. eucomum*, *P. guttatum*, *P. erianthum*, *P. sanguinolentum*, *P. ammodes*, *P. polyphyllum*, and *P. blepharophorum* (= *P. polyphyllum*); and sections *Cristati*, *Genuini*, *Axonopodes*, and *Ceresiae*, with *P. pyramidalis* (= *P. repens*) and *P. stellatum*.

Doell (1877) grouped *Paspalum* into three sections: sect. *Eremachyrion*, sect. *Emprosthion*, and sect. *Opistion*, including in section *Opistion* the fol-

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lowing species: *Paspalum aspidiotes* (subg. *Ceresia*), *P. pectinatum* (subg. *Ceresia*), *P. eucomum* (subg. *Ceresia*), *P. blepharophorum* (= *P. humboldtianum*, subg. *Ceresia*), *P. ammodes* (group Eriantha), *P. guttatum* (group Eriantha), *P. sanguinolentum* (group Eriantha), *P. erianthum* (group Eriantha), *P. stellatum* (subg. *Ceresia*), *P. membranaceum* (= *P. ceresia*, subg. *Ceresia*), *P. heterotrichon* (subg. *Ceresia*), *P. trachycoleon* (subg. *Ceresia*), *P. lanciflorum* (subg. *Ceresia*), and *P. carinatum* (subg. *Ceresia*).

Bentham (1881) considered three sections in *Paspalum*: sect. *Anastrophus*, sect. *Cabrera*, and sect. *Eupaspalum*, the first two characterized by the presence of distichous spikelets with the lower lemma facing the axis, while in section *Eupaspalum* spikelets are unilateral with the lower lemma outward from the axis of the raceme. Within section *Eupaspalum*, Bentham (1881) distinguished four subsections: subsect. *Anachyris*, as an artificial group with a single bract below the upper anthecium; subsect. *Ophistion*, with species without a foliaceous rachis; subsect. *Seudoceresia*, with a rachis more or less foliaceous, green, and concave with glabrous and small spikelets (including such species as *P. stoloniferum* and *P. repens*); and subsect. *Ceresia*, characterized by its foliaceous rachis, with the margins membranous and colored, spikelets ciliate and larger. Within subsection *Ceresia*, Bentham included many tropical species and also *P. cymbiforme*.

Pilger (1929) divided *Paspalum* into eight sections: sect. *Eupaspalum*, sect. *Anachyris*, sect. *Pterolepidium*, sect. *Erianthum*, sect. *Cymatochloa*, sect. *Ceresia*, sect. *Eriolepidium*, and sect. *Moenchia*. This author treated in section *Ceresia* such species as *P. membranaceum* (= *P. ceresia*), *P. stellatum*, *P. heterotrichon*, *P. carinatum*, *P. eucomum*, *P. pectinatum*, *P. cordatum*, *P. humboldtianum*, and *P. trachycoleon*.

Chase (1929), in her study of North American species of *Paspalum*, related subgenus *Ceresia* with her group Dissecta, both with the rachis of the racemes foliaceous and winged, separating Dissecta by the presence of glabrous spikelets. Among the species included by Chase in her treatment are: *Paspalum pectinatum*, *P. contractum* (= *P. lanciflorum*), *P. stellatum*, *P. heterotrichon*, *P. trachycoleon*, *P. cymbiforme*, and *P. humboldtianum*. Chase (1929) stressed that *P. sanguinolentum* (excluded here) did not belong to subgenus *Ceresia* but to group Eriantha. Later, Chase (ined.) placed in subgenus *Ceresia P. carinatum*, *P. ceresia*, *P. heterotrichon*, *P. stellatum*, *P. trachycoleon*, *P. phyllorhachis*, *P. soboliferum* (= *P. humboldtianum*), *P. polyphyllum*, *P. humboldtianum*, *P. humboldtianum* var. *stuckertii* (= *P. humboldtianum*), *P. buchtienii*, *P. malmeanum*, *P. eucomum*, *P. splendens* (= *P. eucomum*), *P. guttatum*, and *P. ammodes*. On the other hand, *Paspalum aspidiotes*, *P. pectinatum*, *P. cordatum*, *P. setiglume*, *P. contractum*, and *P. lanciflorum* were grouped in section *Pectinata* (see Table 4 for groups considered here).

Clayton and Renvoize (1986) recognized eight sections within *Paspalum*: sect. *Diplostachys*, sect. *Pterolepidium*, sect. *Anachyris*, sect. *Erianthum*, sect. *Eriolepidium*, and sect. *Moenchia* with a triquetrous, not membranous, rachis; sect. *Paspalum* and sect. *Ceresia* with a membranous or foliaceous, winged rachis. Section *Ceresia* was distinguished (Clayton & Renvoize, 1986) by including species with a membranous, colorful rachis, and spikelets with the upper glume and lower lemma scabrous, usually ciliate, sometimes winged.

Rodríguez (1992) established *Paspalum* sect. *Pectinata* and distinguished it from section *Ceresia* by including species with spikelets winged and broadly ovoid, cordiform or not at the base.

Filgueiras and Davidse (1994) described, within *Paspalum* subg. *Ceresia*, section *Biaristata*, including two species: *P. biaristatum* and *P. longiaristatum*, both defined by conspicuous awns on the upper glume and lower lemma.

Most recently, Rodríguez (1998) made an account of nine species of *Paspalum* subg. *Ceresia* for Venezuela: *P. setiglume*, *P. pectinatum*, *P. lanciflorum*, *P. carinatum*, *P. humboldtianum*, *P. polyphyllum*, *P. stellatum*, *P. trachycoleon*, and *P. heterotrichon*, all with a winged rachis and pilose spikelets.

Materials and Methods

Morphological Analysis

Specimens were examined from the following herbaria: B, BAA, BM, COL, CONC, CTES, G, IBGE, K, LE, LIL, LPB, MA, MEXU, MO, P, R, RB, SI, UB, US, W (Holmgren et al., 1990; Appendix 2). A list of specimens examined for the outgroup taxa is provided in Appendix 3. Scanning electron micrographs (SEMs) were prepared of the upper anthecium of six species, utilizing the procedures described by Soderstrom and Zuloaga (1989). The vouchers for this SEM study are marked with an asterisk in Appendix 2; the type specimen of *P. reticulinerve*, *Solomon 17003*, was also used. The specimens were viewed on a Zeiss 940 A scanning electron microscope of the Darwinion institute, operating at 10–20 kV.

Phylogenetic Analysis

Characters. Fifty-eight exomorphological characters were used in the cladistic analysis; 15 char-

Table 1. Morphological characters and character states used for the cladistic analysis of *Paspalum* subg. *Ceresia*.

Life form

1. Life cycle: perennial (0), annual (1). This character is a synapomorphy for group Racemosa in *Paspalum*. Annual species in section *Ceresia* are *Paspalum longiaristatum* and *P. cachimboense*.
2. Habit: terrestrial (0), aquatic or subaquatic plants (1).
3. Culms with spongy pith: absent (0), present (1).

Both characters 2 and 3 are helpful to solve relationships within the outgroup.

Blades

4. Shape: linear-lanceolate (0), linear (1).
5. Basal leaves: not pseudopetiolate (0), shortly pseudopetiolate (1), markedly pseudopetiolate (2). *Paspalum buchtienii*, *P. cymbiforme*, and *P. humboldtianum* have shortly pseudopetiolate leaves, with the pseudopetiole a narrowed zone at the base of the blade. Markedly pseudopetiolate leaves is an autapomorphy for *P. imbricatum*, where leaves have a long narrowed zone between the collar and the flattened blade, both about the same length.

Inflorescenses

First-order branching of species here treated in *Panicum* and *Anthaenantiopsis* are considered homologous to unilateral racemes in *Paspalum*.

6. Spikelets unilaterally arranged on the rachis: absent (0), present (1). Unilaterally arranged spikelets are present in all studied species of *Paspalum*.
7. Truncate inflorescences: absent (0), present (1). The inflorescence is truncate when its main axis does not end in a spikelet, and the most distal raceme is a first order branch.
8. Raceme number per inflorescence: 1 (0), 2 (1), 3 or more racemes (2).
9. Arrangement of racemes: solitary (0), conjugate (1), subdigitate (2), alternate (3). Racemes are conjugate when the internode between two contiguous racemes is almost absent; when these internodes are short, up to 1 cm long, racemes are subdigitate; finally, when the internodes are well developed, racemes are considered as alternate.
10. Rachis of the racemes: triquetrous (0), winged with longitudinal veins at the wings (1), winged with anastomosed veins at the wings (2), winged and nerveless, with hyaline to membranous wings (3). The rachis was scored as triquetrous when the ventral side has the same development of the lateral margins, while it was considered as winged when the lateral margins are clearly developed and flat. Nerveless and hyaline to membranous wings only occurs in some species of *Paspalum* subg. *Ceresia*.
11. Rachis of the racemes: ending in a spikelet (0), in a naked point (1), in both a spikelet or in a naked point (2). Within subgenus *Ceresia*, and group Racemosa in *Paspalum*, the rachis usually ends in a sterile prolongation. Nevertheless, the rachis ends both in a spikelet or in a naked point in several species of the subgenus, while in *P. goyasense* it always ends in a developed spikelet.
12. Rachis disarticulating at maturity: absent (0), present (1). This character is a synapomorphy of the Racemosa group.

Table 1. Continued.

13. Pedicels laterally inserted in the spikelets: absent (0), present (1). This feature is present in *Paspalum heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis*, where a scar is noticeable at the lateral base of the upper glume (Fig. 1F, 2F).

Spikelets

14. Shape: biconvex (0), plano-convex (1). Plano-convex spikelets are a synapomorphy within the studied species of *Paspalum*.
15. Disposition: solitary (0), paired (1), paired with the lower spikelet reduced or aborted (2), with 3 or more spikelets together (3). When the inner spikelet is reduced or aborted, evidence of the paired condition is seen in the presence of the lower pedicel. Two, three, or more spikelets are present on one branch in *Panicum laxum* and *P. obtusum*.
16. Spikelets with an annular thickening at the base: absent (0), present (1). This character is present in *Paspalum heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis*.

Lower Glume

17. Presence: present (0), absent (1). The lack of a lower glume is a synapomorphy of the studied species of *Paspalum*.

Upper glume

18. Texture: hyaline (0), membranous (1). We consider the upper glume as hyaline when light passes through it, and membranous when it does not.
19. Winged upper glume: absent (0), present (1). A winged upper glume has flat and extending margins. This character is shared by species of section *Pectinata*, with the exception of *Paspalum lanciflorum* and *P. cachimboense*.
20. Base cordate: absent (0), present (1). As in the previous character, this feature is present in section *Pectinata* (but not in *Paspalum lanciflorum* and *P. cachimboense*).
21. Apex: not awned (0), awned (1). Awned glumes are present in *Paspalum longiaristatum* and *P. biaristatum*.
22. Corky margins: absent (0), present (1); usually found in *Paspalum buchtienii*, *P. cymbiforme*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*.
23. Ciliate margins: absent (0), present (1). We consider that the margins are ciliate when they have short, rigid, and setose hairs in only one series. *Paspalum reticulinerve* and *P. aspidiotes*.
24. Pilose margins: absent (0), present (1). Marginal hairs are long, not rigid, and arranged in several series.
25. Radiate marginal hairs: absent (0), present (1). When marginal hairs are radiate, they look like a crown, as in *Paspalum buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*.
26. Surface pilosity: absent (0), hairs basal, arising from a basal point (1), hairs present in the lower half of the upper glume (2), hairs all over the surface of the upper glume (3). Hairs are usually found in *Paspalum* subg. *Ceresia* in the basal portion and margins of the upper glume; they are less frequent in the distal portion.

Table 1. Continued.

27. Numbers of nerves: 2 (0), 3 (1), 5 (2), 7 (3).
28. Disposition of nerves: equidistant (0), lateral nerves near the margins (1). This character is helpful to resolve relationships within outgroups.
29. Position of lateral nerves: marginal (0), submarginal (1).
30. Lateral extension of the margins: flat (0), curved after the nerve (1), plicate along the nerve (2), absent (3). We considered a lateral extension present when the margin continues after the lateral nerve.
31. Marginal nerves only present in the lower half of the upper glume: absent (0), present (1). This is a common character for species of section *Pectinata*, with the exception of *Paspalum lanciflorum* and *P. cachimboense*.
32. Anastomosed veins in the upper glume: absent (0), present (1). This is a character observed in *Paspalum reticulinerve* and *P. aspidiotes*.
33. Base horseshoe-shaped: absent (0), present (1). This is observed in *Paspalum buchtienii* and *P. humboldtianum*, both species with basal margins extended.

Lower floret

34. Lower floret: present, staminate (0), absent (1). The absence of a lower floret is a synapomorphy of *Paspalum*.

Lower lemma

35. Texture: hyaline (0), membranous (1).
36. Wings: absent (0), present (1). Wings on the lower lemma were considered present when the margin of the lower lemma is flat and extended, as in *Paspalum reticulinerve*, *P. imbricatum*, and *P. aspidiotes*.
37. Base: rounded (0), subcordate (1), cordate (2). A cordate lower lemma was observed in *Paspalum imbricatum* and *P. aspidiotes*, while it is subcordate in *P. pectinatum* and *P. cordatum*.
38. Apex: not awned (0), awned (1). An awned apex of the lower lemma is found in *Paspalum longiaristatum* and *P. biaristatum*.
39. Ciliate margins: absent (0), present (1). As in character 23, the lower lemma margins are considered ciliate when these appendages are short, rigid, setose, and arranged in one series along the margins, as in *Paspalum reticulinerve* and *P. aspidiotes*.
40. Margin pilosity: absent (0), present (1).
41. Tuberculate, marginal hairs: absent (0), present (1). This is a character observed in *Paspalum lanciflorum*, *P. cachimboense*, *P. pectinatum*, and *P. cordatum*.
42. Surface pilosity: absent (0), present (1).
43. Number of nerves: 2 (0), 3 (1), 5 (2).
44. Disposition of the nerves: equidistant (0), lateral nerves near the margins (1). This character is helpful to resolve relationships within outgroups.
45. Disposition of lateral nerves: marginal (0), submarginal (1).
46. Lateral extension of the margins: flat (0), curved after the nerve (1), plicate along the marginal nerve (2), absent (3). See character 30.
47. Marginal nerves only present in the lower half of the lower lemma: absent (0), present (1). One or two marginal nerves, which do not reach the apex, are present in *Paspalum imbricatum* and *P. aspidiotes*.

Table 1. Continued.

48. Relative length of upper glume and lower lemma: both bracts of the same length (0), upper glume longer (1), lower lemma longer (2).

Upper anthecium

49. Shape: ovoid to lanceolate (0), obovoid (1).
50. Stipe: absent (0), present (1). A stipe is present in *Paspalum lanciflorum*, *P. cachimboense*, *P. aspidiotes*, and *P. stellatum*.
51. Texture: hyaline (0), membranous (1), chartaceous (2).
52. Upper palea gap at the apex: not gaping, when the upper lemma encloses the apex of the palea (0), gaping, when the apex of the palea is free (1). All species of *Paspalum* subg. *Ceresia* have an open upper anthecium.
53. Relative length of the anthecium and the spikelet: equal (0), upper anthecium shorter than the spikelet (1).
54. Papillae at the upper lemma: absent (0), simple papillae (1), verrucose papillae (2). A simple papilla is an epidermic prominence including the cellular lumen, and a verrucose papilla is a papilla with additional prominences on the surface (Arriaga, 1987). Verrucose papillae are found in *Paspalum guttatum*, in the Eriantha outgroup, and in some specimens of *P. stellatum* within *Paspalum* subg. *Ceresia*.
55. Silica bodies at the upper lemma: absent (0), present (1).
56. Unicellular macrohairs at the upper lemma: absent (0), present (1).
57. Bicellular microhairs at the upper lemma: absent (0), present (1).
58. Lodicules: present (0), absent (1). Lodicules are absent in *Paspalum ceresia*, *P. longiaristatum*, and *P. biaristatum*.

acters are multistate and were treated as unordered; 11 of these characters were uninformative since they did not show variation within the ingroup. Table 1 provides the list of characters used in the analysis. Autapomorphies were excluded from the analysis. The data matrix is shown in Table 2. Some potentially informative characters were left out of the analysis, either because of the large amount of intraspecific variation, the lack of enough material, or because it was extremely difficult to score them due to overlapping states in different species, e.g., spikelet length and width, rachis width, and blade pilosity.

Cladistic analysis. The cladistic analysis was based on maximum parsimony using NONA version 2.0 (Goloboff, 1997a) under equal weights. Due to the large number of terminals, a heuristic analysis was run following command sequence: "hold10000; rseed 0; hold/40; poly = ; amb-; mult*100; max*; sswap*." One hundred subsearches were performed, each constructing a Wagner tree using a random addition sequence, swapping the initial tree with TBR

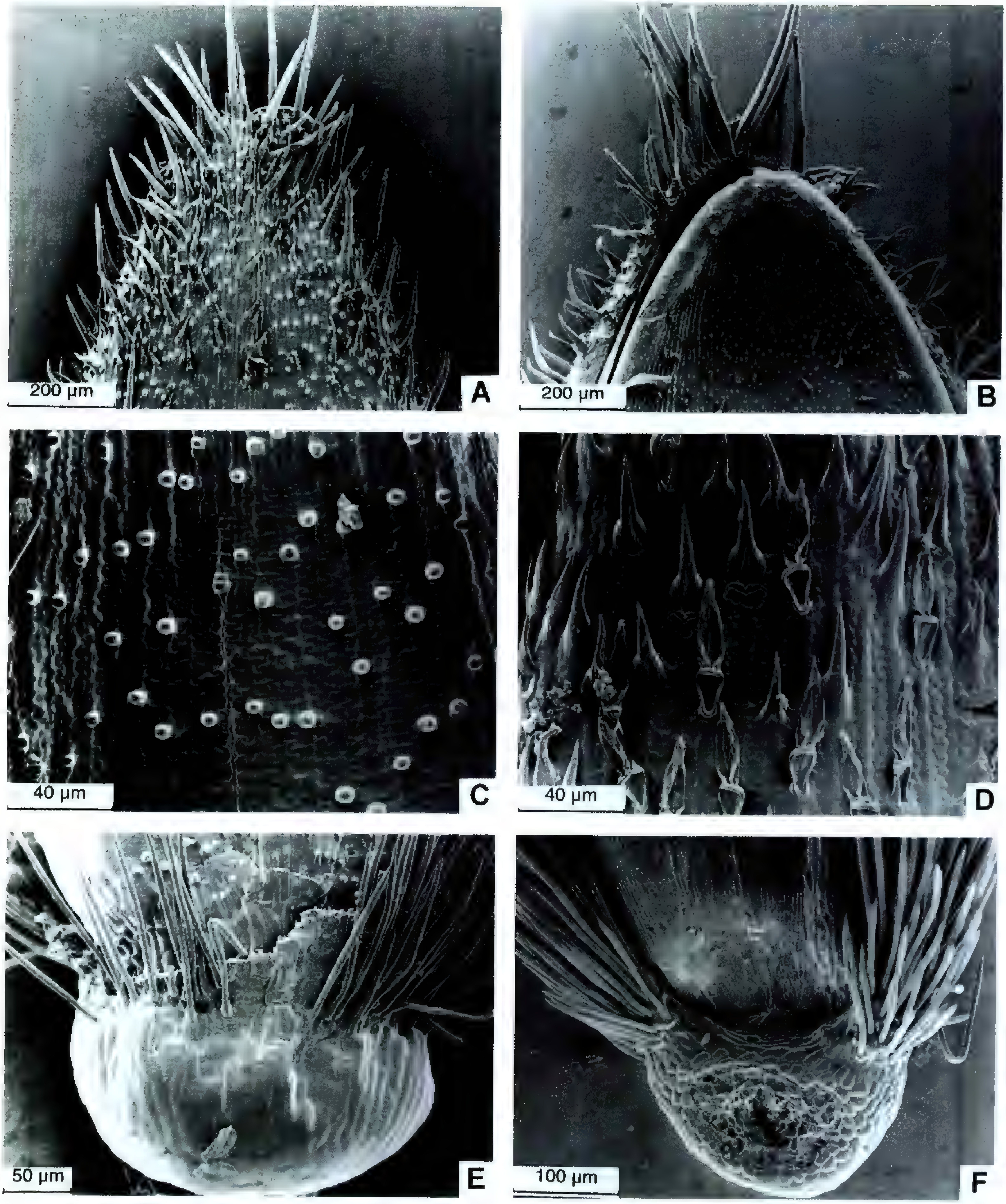

Figure 1. Scanning electron micrographs of the upper anthecium of *Paspalum*.—A. *P. pectinatum*, apex of the upper lemma (*Dusén 16057*, SI). —B. *P. reticulinerve*, apex of the upper palea (*Solomon 17003*, MO). —C. *P. trachycoleon*, upper palea with simple papillae (*Tamayo 2016*, US). —D. *P. biaristatum*, upper palea with bicellular microhairs, macrohairs (*Oliveira 758*, SI). E, F. *P. trachycoleon*.—E. Spikelet base, dorsal view (*Tamayo 2016*, US). —F. Spikelet base, ventral view (*Filgueiras 3567*, SI).

(tree bisection-reconnection) and retaining a maximum of 40 trees in each replication. The resulting trees were swapped using one round of TBR (max*) and one round of "sswap*," which performed TBR swapping cutting two sister nodes simultaneously. The default option "amb-" retained only nodes that are supported by unambiguous optimizations, while poly = treats trees as polytomous.

Table 2. Data matrix used in the cladistic analysis. Polymorphic character states are scored as: A = [01]; B = [02]; C = [03]; D = [12]; E = [23]; F = [012]; G = [013]; H = [023]; I = [123]. Dashes indicate character inapplicable for a taxon.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Panicum laxum	0	0	0	0	0	1	0	2	3	0	0	0	0	0	G	0	0	1	0
Panicum obtusum	0	0	0	0	0	0	0	2	3	0	0	0	0	0	G	0	0	1	0
Anthaenantiopsis fiebrigii	0	0	0	0	0	1	0	2	3	0	0	0	0	0	1	0	0	1	0
Paspalum acuminatum	0	1	1	0	0	1	1	F	H	1	0	0	0	1	0	0	1	0	0
P. almum	0	0	0	0	0	1	1	D	I	1	0	0	0	1	0	0	1	1	0
P. candidum	1	0	0	0	0	1	1	2	3	2	1	1	0	1	0	0	1	—	—
P. cromyorrhizon	0	0	0	1	0	1	1	D	2	0	0	0	0	1	0	0	1	1	0
P. dissectum	0	1	1	0	0	1	1	2	3	2	0	0	0	1	0	0	1	A	0
P. erianthum	0	0	0	0	0	1	1	2	E	1	0	0	0	1	1	0	1	0	0
P. guttatum	0	0	0	1	0	1	1	F	F	1	0	0	0	1	0	0	1	1	0
P. notatum	0	0	0	0	0	1	1	D	D	0	0	0	0	1	0	0	1	1	0
P. prostatum	1	0	0	0	0	1	1	2	E	2	1	1	0	1	0	0	1	1	0
P. racemosum	1	0	0	0	0	1	1	2	E	2	1	1	0	1	0	0	1	1	0
P. sanguinolentum	0	0	0	0	0	1	1	D	3	1	0	0	0	1	2	0	1	1	0
P. aspidiotes	0	0	0	0	0	1	1	2	3	3	1	0	0	1	0	0	1	1	1
P. biaristatum	0	0	0	1	0	1	1	F	C	3	1	0	0	1	0	0	1	0	0
P. buchtienii	0	0	0	0	1	1	1	2	E	1	2	0	0	1	2	0	1	A	0
P. burmanii	0	0	0	0	0	1	1	2	3	2	2	0	0	1	1	0	1	1	0
P. cachimboense	1	0	0	0	0	1	1	F	2	3	1	0	0	1	0	0	1	1	0
P. carinatum	0	0	0	1	0	1	1	A	C	3	1	0	0	1	0	0	1	1	0
P. ceresia	0	0	0	A	0	1	1	F	C	3	1	0	0	1	0	0	1	A	0
P. cordatum	0	0	0	1	0	1	1	2	2	1	1	0	0	1	0	0	1	1	1
P. cymbiforme	0	0	0	0	1	1	1	F	C	3	1	0	0	1	2	0	1	A	0
P. eucomum	0	0	0	1	0	1	1	D	D	3	1	0	0	1	0	0	1	1	0
P. goyasense	0	0	0	0	0	1	1	F	C	3	0	0	0	1	0	0	1	1	0
P. heterotrichon	0	0	0	0	0	1	1	F	C	3	1	0	1	1	0	1	1	0	0
P. humboldtianum	0	0	0	0	1	1	1	D	3	1	2	0	0	1	2	0	1	0	0
P. imbricatum	0	0	0	0	2	1	1	D	E	3	1	0	0	1	0	0	1	1	1
P. lanciflorum	0	0	0	0	0	1	1	F	B	3	1	0	0	1	0	0	1	1	0
P. longiaristatum	1	0	0	1	0	1	1	F	C	3	1	0	0	1	0	0	1	0	0
P. malmeanum	0	0	0	1	0	1	1	A	A	3	1	0	0	1	0	0	1	1	0
P. niquelandiae	0	0	0	0	0	1	1	2	3	1	2	0	0	1	1	0	1	1	0
P. pectinatum	0	0	0	0	0	1	1	D	D	3	1	0	0	1	0	0	1	A	1
P. petrense	0	0	0	0	0	1	1	2	3	2	1	0	1	1	2	1	1	A	0
P. phyllorhachis	0	0	0	0	0	1	1	2	3	2	1	0	1	1	1	1	1	A	0
P. polyphyllum	0	0	0	A	0	1	1	F	C	2	2	0	0	1	2	0	1	0	0
P. reticulinerve	0	0	0	0	0	1	1	D	D	1	1	0	0	1	1	0	1	1	1
P. stellatum	0	0	0	1	0	1	1	A	A	3	1	0	0	1	0	0	1	1	0
P. trachycoleon	0	0	0	0	0	1	1	2	3	2	1	0	1	1	1	1	1	A	0

Tests to evaluate homoplasy were consistency index (CI) and retention index (RI) (Farris, 1989).

Two strategies were carried out in an attempt to find possible islands for MP trees (Maddison, 1991). First, command "jump*3" was used, which performs TBR swapping on trees up to 3 steps longer than initial trees (Goloboff, 1993). The second strategy was carried out using "hold/5; mult*400," which performed 400 independent searches beginning from different Wagner trees.

Bremer support (Bremer, 1994) and jackknife group frequencies (Farris et al., 1996) were conducted in order to calculate branch support with NONA. Commands used for Bremer support were "subN; hold1500; find*"; bsupport performing TBR swapping on preexisting trees, saving trees up to 4 steps longer at each round. Jackknife frequency values were calculated using the available instruction file for NONA, the JAK.RUN file. One thousand iterations were performed, randomly deleting 36% of the characters, with the search options "mult*5," and the FQ.EXE file was used to cal-

Table 2. Extended.

2 0	2 1	2 2	2 3	2 4	2 5	2 6	2 7	2 8	2 9	3 0	3 1	3 2	3 3	3 4	3 5	3 6	3 7	3 8	3 9
0	0	0	0	0	0	0	D	0	1	1	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	3	0	1	1	0	0	0	0	1	0	0	0	0
0	0	0	0	1	0	3	2	0	1	0	0	0	0	0	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	0	0	0	0	1	0	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	0	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	0	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	2	1	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	3	2	1	1	1	0	0	0	1	1	0	0	0	0
1	0	0	1	0	0	0	3	0	1	0	1	1	0	1	1	1	2	0	1
0	1	0	0	1	0	1	1	0	0	3	0	0	0	1	1	0	0	1	0
0	0	1	0	1	1	2	1	0	1	2	0	0	1	1	1	0	0	0	0
0	0	1	0	1	1	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	1	1	0	0	3	0	0	0	1	0	0	0	0	0
1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	0	1	0	0
0	0	1	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	1	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	3	1	0	1	2	0	0	1	1	1	0	0	0	0
1	0	0	0	0	0	0	2	0	1	0	1	0	0	1	1	1	2	0	0
0	0	0	0	0	0	1	1	0	1	1	0	0	0	1	1	0	0	0	0
0	1	0	0	1	0	1	1	0	0	3	0	0	0	1	1	0	0	1	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	0	1	0	1	2	0	0	0	1	1	0	0	0	0
1	0	0	0	0	0	0	D	0	1	0	1	0	0	1	1	0	1	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	0	0	0	0	0	1	0	1	2	0	0	0	1	1	0	0	0	0
0	0	1	0	1	1	3	1	0	1	2	0	0	0	1	1	0	0	0	0
1	0	0	1	0	0	0	3	0	1	0	1	1	0	1	1	1	0	0	1
0	0	0	0	1	0	1	A	0	0	3	0	0	0	1	1	0	0	0	0
0	0	0	0	1	0	2	1	0	1	2	0	0	0	1	1	0	0	0	0

culate the majority rule consensus trees of the output (Goloboff, 1993).

Separate analysis using implied weights (Goloboff, 1993) was run in PeeWee version 3.0 (Goloboff, 1997b) using the same search strategies as in NONA. PeeWee weights characters according to how well they fit a specific tree. Homoplastic characters were downweighted in proportion to their number of extra steps. We used a medium concave function, K = 3.

Outgroups. In the present treatment we followed Nixon and Carpenter (1993) for selecting the outgroups. Species of *Paspalum* that share potential synapomorphies with those of subgenus *Ceresia* were included as outgroups: taxa of the Dissecta, Eriantha, Racemosa, and Notata groups in *Paspalum* were chosen because they share with subgenus *Ceresia* a wide rachis in the inflorescences (Chase, 1929, ined.; Morrone et al., 1995; Zuloaga & Morrone, in prep.). Therefore, *P. acuminatum* and *P. dissectum*, of group Dissecta, *P. erianthum*, *P. guttatum*, and *P. sanguinolentum* of group Eriantha, *P.*

Table 2. Continued.

Character	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58
Panicum laxum	0	0	0	D	0	1	1	0	0	0	0	D	0	0	0	0	1	0	0
Panicum obtusum	0	0	0	2	0	1	1	0	2	0	0	2	0	0	0	1	0	1	0
Anthaenantiopsis fiebrigii	1	0	1	2	0	1	1	0	2	0	0	1	1	0	1	1	1	1	0
Paspalum acuminatum	0	0	0	2	1	1	0	0	0	0	0	2	0	1	1	1	1	1	0
P. almum	0	0	0	2	1	1	2	0	0	0	0	2	0	1	1	0	0	0	0
P. candidum	0	0	0	1	0	1	0	0	—	0	0	D	0	0	1	1	0	0	0
P. cromyorrhizon	0	0	0	2	1	1	2	0	0	0	0	D	0	1	1	1	0	1	0
P. dissectum	0	0	0	2	1	1	1	0	0	1	0	2	0	0	1	1	0	0	0
P. erianthum	1	0	1	1	0	1	1	0	0	0	0	2	0	1	1	0	0	1	0
P. guttatum	1	0	1	1	0	1	0	0	0	0	0	2	0	1	2	1	0	1	0
P. notatum	0	0	0	2	1	1	2	0	0	0	0	2	0	1	1	0	0	1	0
P. prostatum	0	0	0	1	0	1	1	0	0	0	0	2	0	0	1	0	0	1	0
P. racemosum	0	0	0	1	0	1	1	0	0	0	0	2	0	1	0	1	0	0	0
P. sanguinolentum	1	0	1	2	1	1	1	0	0	0	0	2	0	0	1	1	0	1	0
P. aspidiotes	0	0	0	2	0	1	0	1	1	0	1	1	1	1	1	1	1	1	0
P. biaristatum	1	0	1	1	0	0	3	0	1	0	0	1	1	1	0	0	1	1	1
P. buchtienii	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. burmanii	0	0	0	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0
P. cachimboense	1	1	0	1	0	1	2	0	0	0	1	1	1	1	1	0	1	1	0
P. carinatum	1	0	1	1	0	1	1	0	1	0	0	1	1	1	1	0	1	1	0
P. ceresia	1	0	1	0	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1
P. cordatum	1	1	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
P. cymbiforme	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. eucomum	1	0	1	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0
P. goyasense	1	0	1	1	0	1	1	0	A	0	0	D	1	1	1	0	1	0	0
P. heterotrichon	1	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	1	1	0
P. humboldtianum	0	0	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. imbricatum	0	0	0	2	0	1	0	1	B	0	0	1	1	1	1	0	1	1	0
P. lanciflorum	1	1	0	1	0	1	2	0	1	0	1	1	1	1	1	1	0	1	0
P. longiaristatum	1	0	1	1	0	0	3	0	1	0	0	1	1	1	0	1	1	1	1
P. malmeanum	1	0	1	1	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0
P. niquelandiae	0	0	0	1	0	1	1	0	0	0	0	D	1	0	1	0	0	1	0
P. pectinatum	1	1	1	1	0	1	0	0	1	0	0	1	1	1	1	1	1	1	0
P. petrense	1	0	1	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	0
P. phyllorhachis	0	0	0	1	0	1	2	0	0	0	0	1	1	0	1	0	1	1	0
P. polyphyllum	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1	0
P. reticulinerve	0	0	0	1	0	1	0	0	1	0	0	1	1	1	1	0	1	1	0
P. stellatum	1	0	1	0	0	0	3	0	0	1	1	1	1	1	B	0	0	0	0
P. trachycoleon	0	0	0	1	0	1	1	0	0	0	0	1	1	0	1	0	1	1	0

almum, *P. cromyorrhizon*, and *P. notatum* of group Notata, and *P. candidum*, *P. prostatum*, and *P. racemosum* of group Racemosa were included in the present analysis (Table 4).

Panicum obtusum Kunth and *Anthaenantiopsis fiebrigii* Parodi were also included as outgroups due to their relationship with *Paspalum*, stressed by a recent molecular analysis of the tribe (Giussani et al., 2001). Finally, for the purpose of rooting, *Panicum laxum* Sw., a C_3 representative of the $x = 10$ clade of the Paniceae (Giussani et al., 2001) was also considered in this analysis.

MORPHOLOGICAL CHARACTERS

Habit. Species of *Paspalum* subg. *Ceresia* are perennial, rarely annual (in *P. longiaristatum* and *P. cachimboense*). Culms are herbaceous, occasionally lignified (in *P. buchtienii* and *P. humboldtianum*), unbranched or branched at the lower and middle nodes, hollow, and erect or leaning on the vegetation. Blades range from filiform to linear or lanceolate; a short pseudopetiole is present in *P. buchtienii*, *P. humboldtianum*, and *P. cymbiforme*, while *P. imbricatum* is characterized by its long pseudopetiolate blades.

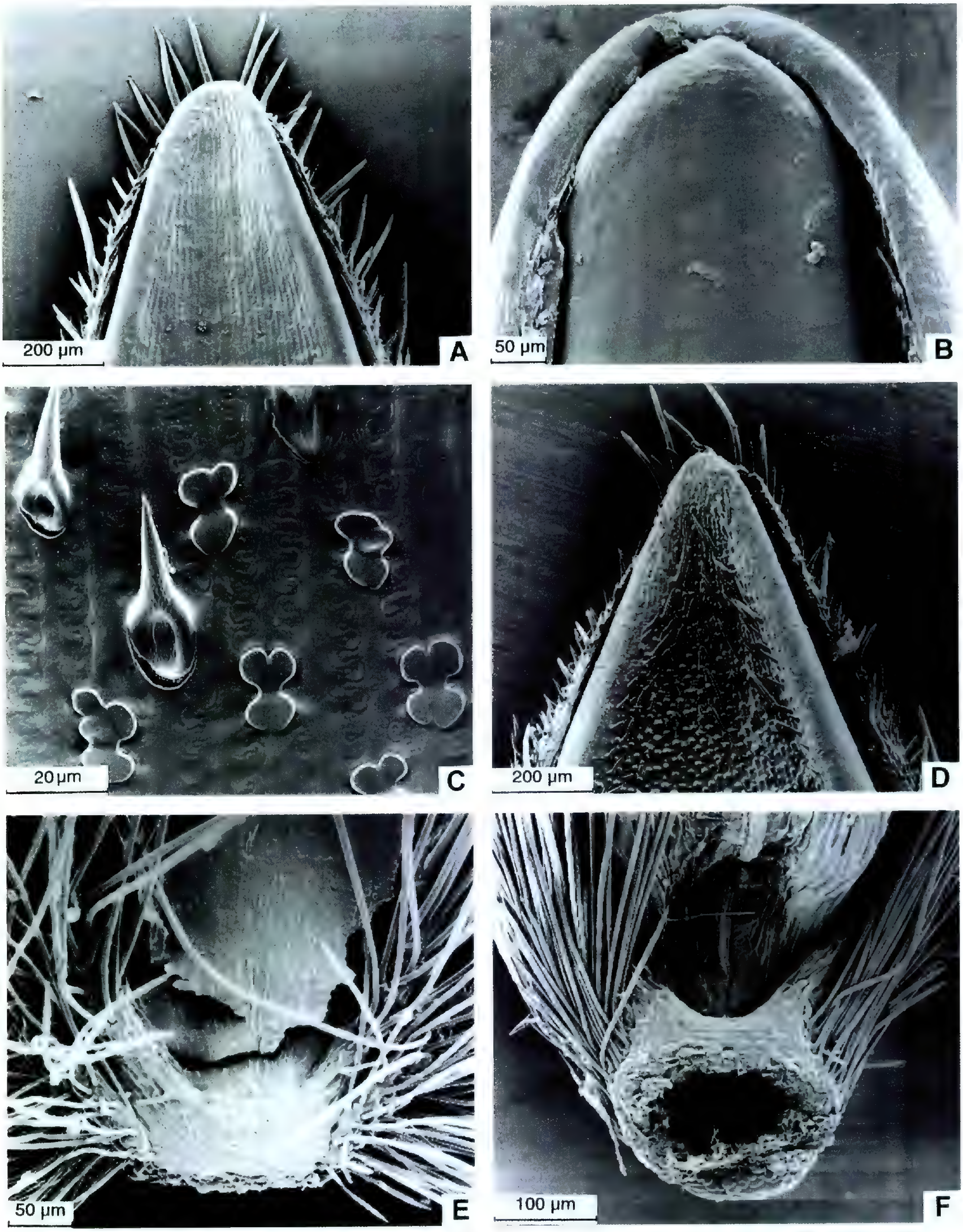

Figure 2. Scanning electron micrographs of the upper anthecium of *Paspalum*.—A. *P. pectinatum*, apex of the upper palea (*Dusén 16057*, SI). —B. *P. malmeanum*, upper palea (*Killeen 2024*, SI). —C. *P. heterotrichon*, upper palea with silica bodies and macrohairs (*Tovar 4176*, US). —D. *P. cordatum*, apex of the upper palea (*Weddell 1699*, P). —E. *P. stellatum*, spikelet base, ventral view (*Killeen 2474*, SI). —F. *P. heterotrichon*, spikelet base, ventral view (*Tovar 4176*, US).

Inflorescences. Inflorescences are usually terminal; axillary inflorescences are common in *Paspalum buchtienii* and *P. polyphyllum.* The number of racemes varies from a single one, e.g., *P. stellatum* and *P. carinatum,* to two conjugate racemes, e.g., *P. malmeanum, P. eucomum, P. reticulinerve,* and *P. pectinatum,* while two alternate racemes are characteristic of *P. goyasense.* When several racemes are present, these can be alternate and distant, e.g., *P. trachycoleon, P. heterotrichon, P. ceresia, P. imbricatum, P. humboldtianum, P. polyphyllum, P. cymbiforme, P. aspidiotes,* and *P. niquelandiae,* or they can be subdigitate (with a short internode, up to 1 cm long, between the racemes) as in *P. cordatum, P. lanciflorum,* and *P. cachimboense.* Pulvini are pilose, and one or two bracts are usually present in *P. stellatum, P. eucomum, P. goyasense, P. malmeanum, P. carinatum,* and *P. pectinatum.*

Rachis of the racemes. Species of *Paspalum* subg. *Ceresia* are typically distinguished by a winged, membranous to foliaceous rachis, 0.8–10 mm wide; the rachis is usually glabrous, occasionally pilose (in *Paspalum polyphyllum*) or ciliate at the margins (in *P. reticulinerve*); hyaline to membranous, and nerveless margins are present in several species, e.g., *P. lanciflorum, P. cachimboense, P. imbricatum, P. pectinatum, P. aspidiotes, P. heterotrichon, P. cymbiforme, P. ceresia, P. stellatum, P. eucomum, P. malmeanum, P. carinatum, P. goyasense, P. biaristatum,* and *P. longiaristatum.*

Although the rachis usually ends in a naked point, in several species, such as *P. humboldtianum, P. buchtienii, P. polyphyllum, P. niquelandiae,* and *P. burmanii,* the rachis finishes in a naked point or in a spikelet; in *P. goyasense* the rachis always ends in a developed spikelet. Spikelets are imbricate and arranged in two or four series.

Spikelets. Spikelets are solitary or paired, dorsiventrally compressed, ranging from ovoid to ellipsoid to lanceolate. The size of spikelets varies from 1.4 to 8 mm in length; they are usually covered with indument, otherwise ciliate; glabrous spikelets are found in *Paspalum phyllorhachis* and *P. imbricatum.* Awned bracts are present only in *P. longiaristatum* and *P. biaristatum.* The lower glume is always absent, while the upper glume is usually as long as the spikelet and 3- to 5-nerved, 7(–9)-nerved in *P. aspidiotes* and *P. reticulinerve,* occasionally 2-nerved in *P. stellatum.* Also, the upper glume is cordate and winged in *P. imbricatum, P. reticulinerve, P. aspidiotes, P. cordatum,* and *P. pectinatum.* The lower lemma is winged in *P. imbricatum, P. reticulinerve,* and *P. aspidiotes.* A lower palea and lower flower are always absent.

Upper anthecium (Figs. 1, 2). The upper anthecium is planoconvex, ellipsoid, ovoid or obovoid, usually hyaline to membranous, but membranous to chartaceous in *Paspalum niquelandiae* and *P. goyasense.* Margins of the upper lemma are flat, not enclosing the apex of the upper palea. A short stipe is present in *P. stellatum, P. lanciflorum, P. cachimboense,* and *P. aspidiotes.*

Regarding the upper anthecium ornamentation, simple papillae regularly distributed, bicellular microhairs and macrohairs, more densely placed toward the apex of the upper lemma and palea, are common features of most species in subgenus *Ceresia.* A smooth and glabrous upper anthecium is present in *Paspalum malmeanum, P. eucomum,* and *P. stellatum.* Bicellular microhairs, 50–70 μm long, have a short basal cell and an elongated apical cell. Unicellular macrohairs, present or absent in subgenus *Ceresia,* can be short and hooked, ca. 40 μm long, to long and thin, 60–300 μm long. Rounded or elongated silica bodies are frequent in several species; these silica bodies have usually 2 to 4 constrictions; 6 or more invaginations are present in *P. lanciflorum.*

Distribution and Habitat

Species of *Paspalum* subg. *Ceresia* grow in America, ranging from Mexico, Mesoamerica, and the Caribbean (Haiti, the Dominican Republic, and Trinidad and Tobago), to South America (Colombia, Venezuela, Guyana, Surinam, Brazil, Ecuador, Peru, Bolivia, Paraguay, central Argentina, and Uruguay). Brazil hosts the largest number of species, 22, and endemics, 10, in the subgenus.

Taxa are usually found in limestone, sandy, or rocky soils, in open fields or mountain slopes, from sea level to 3000 m elevation. Several species, such as *P. carinatum, P. lanciflorum,* and *P. pectinatum,* are found in open areas subjected to periodic fires; these species have culms and sheaths adapted to fire. *Paspalum malmeanum* and *P. cordatum* grow in flooded savannas.

Paspalum stellatum, P. pectinatum, and *P. carinatum* are the most widespread species in subgenus *Ceresia. Paspalum stellatum* grows from Mexico to southern Brazil, Paraguay, northeastern Argentina, and Uruguay; *Paspalum pectinatum* is found from Mexico to southern Brazil, and *P. carinatum* from Nicaragua to Brazil and Trinidad and Tobago. Regarding the biogeographical distribution of subgenus *Ceresia,* species are common in cerrados, Atlantic forests, and savannas; they are also present in caatingas of northeastern Brazil and in the Guyana highlands of Guyana and Venezuela; they are

Table 3. List of synapomorphies of the cladogram shown in Figure 4, with character state changes in the 37 nodes and within taxa. Characters in bold are common synapomorphies for all 40 most parsimonious trees.

Nodes 1–37

Node 1: character **55**: 0 ⇒ 1, character **57**: 0 ⇒ 1
Node 2: character 54: 0 ⇒ 1
Node 3: character **7**: 0 ⇒ 1, character **14**: 0 ⇒ 1, character **17**: 0 ⇒ 1, character **34**: 0 ⇒ 1
Node 4: character **11**: 0 ⇒ 1, character **27**: 2 ⇒ 1, character 28: 1 ⇒ 0, character 43: 2 ⇒ 1
Node 5: character 40: 0 ⇒ 1, character **51**: 2 ⇒ 1, character **52**: 0 ⇒ 1, character 56: 0 ⇒ 1
Node 6: character **9**: 3 ⇒ 2
Node 7: character **24**: 0 ⇒ 1, character **26**: 0 ⇒ 2, character **30**: 1 ⇒ 2
Node 8: character **26**: 0 ⇒ 1, character **50**: 0 ⇒ 1
Node 9: character **19**: 0 ⇒ 1, character **20**: 0 ⇒ 1, character **27**: 1 ⇒ 2, character **30**: 1 ⇒ 0, character **31**: 0 ⇒ 1
Node 10: character **42**: 0 ⇒ 1
Node 11: character **36**: 0 ⇒ 1, character **40**: 1 ⇒ 0
Node 12: character **23**: 0 ⇒ 1, character **27**: 2 ⇒ 3, character **32**: 0 ⇒ 1, character **39**: 0 ⇒ 1
Node 13: character **42**: 0 ⇒ 1, character **55**: 0 ⇒ 1
Node 14: character **4**: 0 ⇒ 1
Node 15: character **46**: 1 ⇒ 0, character **54**: 1 ⇒ 0
Node 16: character 49: 0 ⇒ 1, character 56: 1 ⇒ 0, character 57: 1 ⇒ 0
Node 17: character 26: 2 ⇒ 1, character 29: 1 ⇒ 0, character 30: 2 ⇒ 3
Node 18: character 45: 1 ⇒ 0, character 46: 0 ⇒ 3
Node 19: character 18: 1 ⇒ 0, character **21**: 0 ⇒ 1, character **38**: 0 ⇒ 1, character 48: 0 ⇒ 1
Node 20: character **18**: 1 ⇒ 0
Node 21: character 13: 0 ⇒ 1, character 16: 0 ⇒ 1
Node 22: character 10: 3 ⇒ 2
Node 23: character 40: 1 ⇒ 0, character **53**: 1 ⇒ 0, character **55**: 1 ⇒ 0
Node 24: character **22**: 0 ⇒ 1, character 40: 1 ⇒ 0
Node 25: character **11**: 1 ⇒ 2, character **25**: 0 ⇒ 1
Node 26: character **33**: 0 ⇒ 1
Node 27: character **53**: 1 ⇒ 0
Node 28: character **15**: 2 ⇒ 1, character **18**: 0 ⇒ 1
Node 29: character **1**: 0 ⇒ 1, character **12**: 0 ⇒ 1
Node 30: character 57: 1 ⇒ 0
Node 31: character 28: 0 ⇒ 1, character 44: 0 ⇒ 1
Node 32: character 9: 3 ⇒ 2, character **30**: 1 ⇒ 2, character **46**: 1 ⇒ 2
Node 33: character 55: 1 ⇒ 0
Node 34: character 10: 0 ⇒ 1
Node 35: character **2**: 0 ⇒ 1, character **3**: 0 ⇒ 1
Node 36: character 24: 0 ⇒ 1, character 26: 0 ⇒ 3, character 40: 0 ⇒ 1, character 42: 0 ⇒ 1
Node 37: character 43: 2 ⇒ 1, character 44: 1 ⇒ 0

Outgroup taxa

Panicum obtusum: character **6**: 1 ⇒ 0, character **27**: 2 ⇒ 3
Anthaenantiopsis fiebrigii: character 24: 0 ⇒ 1, character 26: 0 ⇒ 3, character **30**: 1 ⇒ 0, character 40: 0 ⇒ 1, character 42: 0 ⇒ 1, character 51: 2 ⇒ 1, character **52**: 0 ⇒ 1
Paspalum cromyorrhizon: character **4**: 0 ⇒ 1
P. notatum: no autapomorphies

Table 3. Continued.

P. almum: character 10: 0 ⇒ 1, character **57**: 1 ⇒ 0
P. acuminatum: character **30**: 1 ⇒ 0, character **35**: 1 ⇒ 0, character **46**: 1 ⇒ 0, character **56**: 0 ⇒ 1
P. dissectum: character 10: 1 ⇒ 2, character **49**: 0 ⇒ 1, character **57**: 1 ⇒ 0
P. sanguinolentum: character **15**: 0 ⇒ 2
P. erianthum: character 15: 0 ⇒ 1, character **18**: 1 ⇒ 0, character **35**: 1 ⇒ 0, character **55**: 1 ⇒ 0
P. guttatum: character **4**: 0 ⇒ 1, character **46**: 1 ⇒ 0, character **54**: 1 ⇒ 2
P. prostatum: character **55**: 1 ⇒ 0
P. candidum: character **35**: 1 ⇒ 0, character **46**: 1 ⇒ 0
P. racemosum: character **54**: 1 ⇒ 0

Ingroup taxa: Subg. *Ceresia*

P. lanciflorum: character **56**: 1 ⇒ 0
P. cachimboense: character **1**: 0 ⇒ 1, character **55**: 1 ⇒ 0
P. pectinatum: no autapomorphies
P. cordatum: character **4**: 0 ⇒ 1, character **10**: 3 ⇒ 1
P. imbricatum: character **5**: 0 ⇒ 2
P. reticulinerve: character **10**: 3 ⇒ 1, character **15**: 0 ⇒ 1
P. aspidiotes: character **9**: 2 ⇒ 3, character **50**: 0 ⇒ 1
P. goyasense: character **11**: 1 ⇒ 0, character **57**: 1 ⇒ 0
P. carinatum: character 48: 0 ⇒ 1
P. eucomum: character 48: 0 ⇒ 1
P. malmeanum: character **53**: 1 ⇒ 0
P. ceresia: character **35**: 1 ⇒ 0, character **51**: 1 ⇒ 0, character **53**: 1 ⇒ 0, character 55: 0 ⇒ 1
P. stellatum: character 49: 0 ⇒ 1, character **50**: 0 ⇒ 1, character 56: 1 ⇒ 0, character 57: 1 ⇒ 0
P. longiaristatum: character **1**: 0 ⇒ 1, character 55: 0 ⇒ 1
P. biaristatum: no autapomorphies
P. heterotrichon: character **26**: 2 ⇒ 1, character **54**: 1 ⇒ 0
P. petrense: character **42**: 0 ⇒ 1
P. trachycoleon: no autapomorphies
P. phyllorhachis: character **24**: 1 ⇒ 0, character **26**: 2 ⇒ 0, character **46**: 1 ⇒ 2
P. cymbiforme: no autapomorphies
P. buchtienii: no autapomorphies
P. humboldtianum: character **26**: 2 ⇒ 3
P. polyphyllum: character **26**: 2 ⇒ 3, character **40**: 0 ⇒ 1, character **42**: 0 ⇒ 1
P. niquelandiae: character **26**: 2 ⇒ 0, character **55**: 1 ⇒ 0, character **56**: 1 ⇒ 0

less frequent in the Amazonian forests. Several species have an Andean distribution: *P. humboldtianum*, from Mexico and Mesoamerica to northwestern and central Argentina; *P. buchtienii* is restricted to mountain slopes of Bolivia and Peru, while *P. cymbiforme* is found in Mexico and Mesoamerica. A disjunct distribution was observed in the following species: *P. polyphyllum*, present in southern and central Brazil, in the states of Rio Grande do Sul and Santa Catarina, southern Paraguay, northeastern Argentina, and Uruguay, and also in Colombia

Table 4. List of species of informal groups of *Paspalum* Eriantha, Dissecta, Notata, and Racemosa used as outgroups in the cladistic analysis and species of *Paspalum* subg. *Ceresia* and its sections *Ceresia* and *Pectinata*.

Outgroups		
Dissecta Group (sensu Morrone et al., 1996)	*Paspalum acuminatum*	
	P. dissectum	
Eriantha Group (sensu Chase. Ined.)	*P. erianthum*	
	P. guttatum	
	P. sanguinolentum	
Notata Group (sensu Canto-Dorow et al., 1996)	*P. almum*	
	P. cromyorrhizon	
	P. notatum	
Racemosa Group (sensu Morrone et al., 1995)	*P. candidum*	
	P. prostatum	
	P. racemosum	
Paspalum subg. *Ceresia*	section *Pectinata*	*P. aspidiotes*
		P. cachimboense
		P. cordatum
		P. imbricatum
		P. lanciflorum
		P. pectinatum
		P. reticulinerve
	section *Ceresia*	*P. biaristatum*
		P. buchtienii
		P. burmanii
		P. carinatum
		P. ceresia
		P. cymbiforme
		P. eucomum
		P. goyasense
		P. heterotrichon
		P. humboldtianum
		P. longiaristatum
		P. malmeanum
		P. niquelandiae
		P. petrense
		P. phyllorhachis
		P. polyphyllum
		P. stellatum
		P. trachycoleon

and Venezuela. *Paspalum cordatum* has been collected in southern Brazil, Amazonia, and Colombia. *Paspalum ceresia* is common in the Andean region from Ecuador to northwestern Argentina, and isolated populations grow in central Brazil, in the states of Goiás, Maranhão, Minas Gerais, and Pará. Finally, *P. trachycoleon* grows from Mexico and Mesoamerica to Colombia and Venezuela and reappears in southern Brazil.

As previously mentioned, a significant concentration of species is found in the cerrados of central Brazil. *Paspalum biaristatum, P. longiaristatum, P. burmanii,* and *P. niquelandiae* are restricted to serpentine soils of the state of Goiás; *P. petrense, P. imbricatum,* and *P. goyasense* are endemic species of this state; *P. cachimboense* was found only in the Serra do Cachimbo, state of Mato Grosso, on the border with the state of Pará, and *P. phyllorhachis* in Minas Gerais. Another species of subgenus *Ceresia* endemic to central Brazil is *P. eucomum*, present in Minas Gerais, São Paulo, Paraná, Goiás, and in the Distrito Federal. It is noteworthy to mention this high number of endemic species in serpentine soils, characterized by high concentrations of nickel, chromium, cobalt, and other minerals (Brooks, 1987), combined with a low percentage of nutrients in these soils. Other endemic grasses were also previously described for this region (see Filgueiras et al., 1993, for a detailed analysis of the area).

Phylogenetic Analysis

The cladistic analysis using NONA resulted in 40 most parsimonious trees, each of 196 steps, found in 84 of 100 replications, with CI = 38 and RI = 68. Searches to find possible islands yielded no additional trees.

Figure 3. Strict consensus tree from 40 most parsimonious cladograms found by NONA. Numbers below branches indicate Bremer support; numbers above branches indicate jackknife values.

Figure 4 shows one of the 40 most parsimonious trees. Unambiguous synapomorphies of each node are listed in Table 3, which indicates if a character state change occurs just in that cladogram or in all equally parsimonious trees.

The strict consensus is shown in Figure 3, with Bremer support values and jackknife frequencies. In this consensus tree, *Paspalum* is monophyletic with *Anthaenantiopsis fiebrigii* or *Panicum obtusum* as sister taxa. Next within *Paspalum*, there is a major clade including the Racemosa group and subgenus *Ceresia*. Relationships of the remaining studied species of the genus, of Eriantha, Notata, and Dissecta groups, are not solved; they are placed in a basal polytomy in the tree. Two different topologies are equally parsimonious when solving this polytomy, according to the placement of species of the group Eriantha.

The clade comprising groups Racemosa and *Ceresia* (Fig. 4, see node 4) is supported in all most

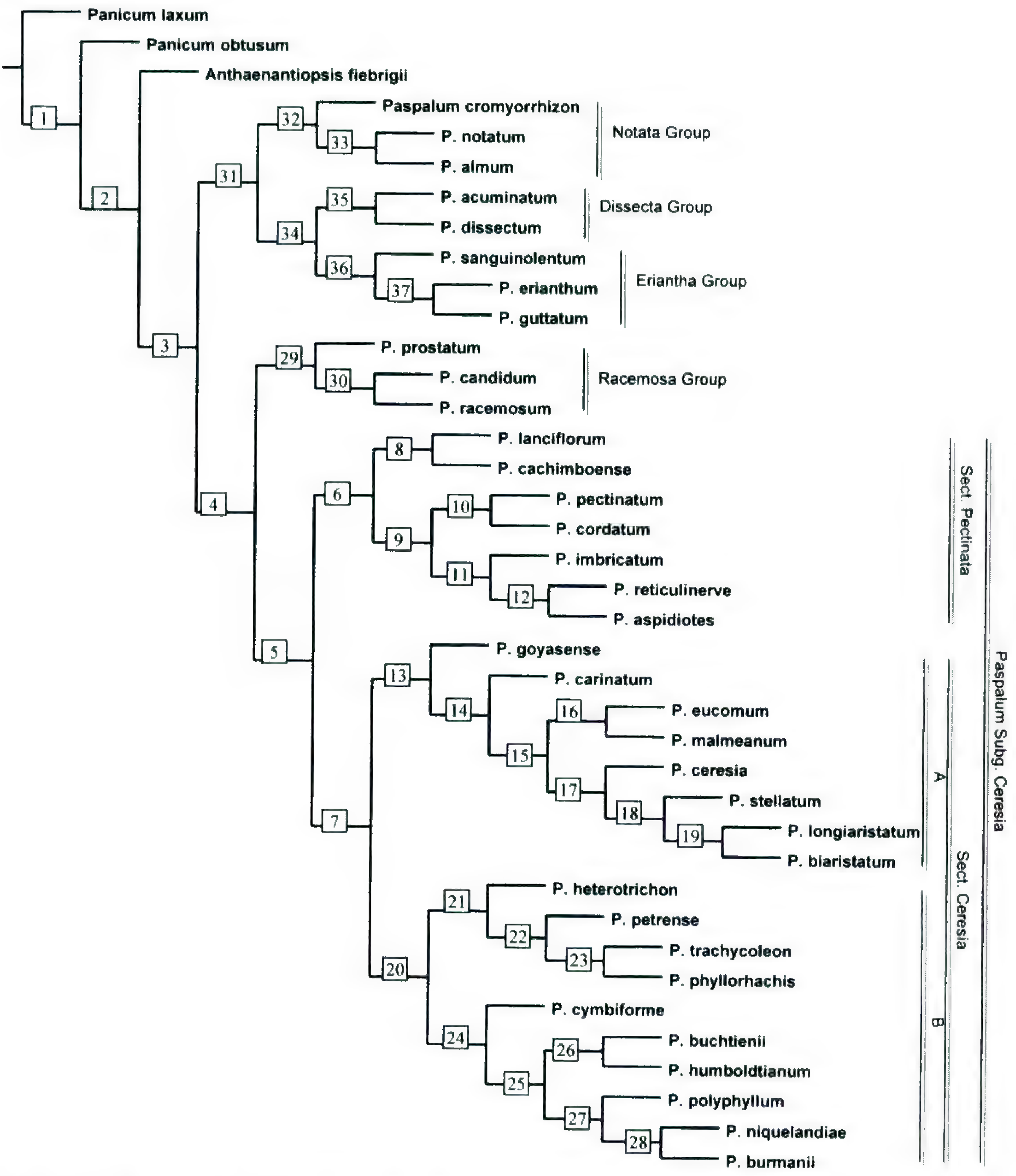

Figure 4. One of the 40 most parsimonious trees found by NONA (196 steps length, CI = 38, RI = 68) with number of nodes in boxes. Synapomorphies of each node and taxa are listed in Table 3.

parsimonious trees by character 11 (apex of the rachis ending in a naked point) and character 27 (upper glume 3-nerved). In some of the most parsimonious trees, character 28 (nerves of the upper glume equidistant) and character 43 (lower lemma 3-nerved) also support this clade.

Paspalum subg. *Ceresia* forms a clade with Racemosa as its sister group. At node 5 (Fig. 4), characters supporting the monophyly of subgenus *Ceresia* are: 51 (membranous upper anthecium) and 52 (upper palea gaping at the apex). Characters 40 (lower lemma with pilose margins) and 56 (upper lemma with unicellular macrohairs) also support subgenus *Ceresia* in some of the most parsimonious trees.

Within *Paspalum* subg. *Ceresia*, two major clades appear in the analysis: one containing species of section *Pectinata*, and the other containing the remaining species of the subgenus. Section *Pectinata* (see node 6, Fig. 4) is supported by character 9

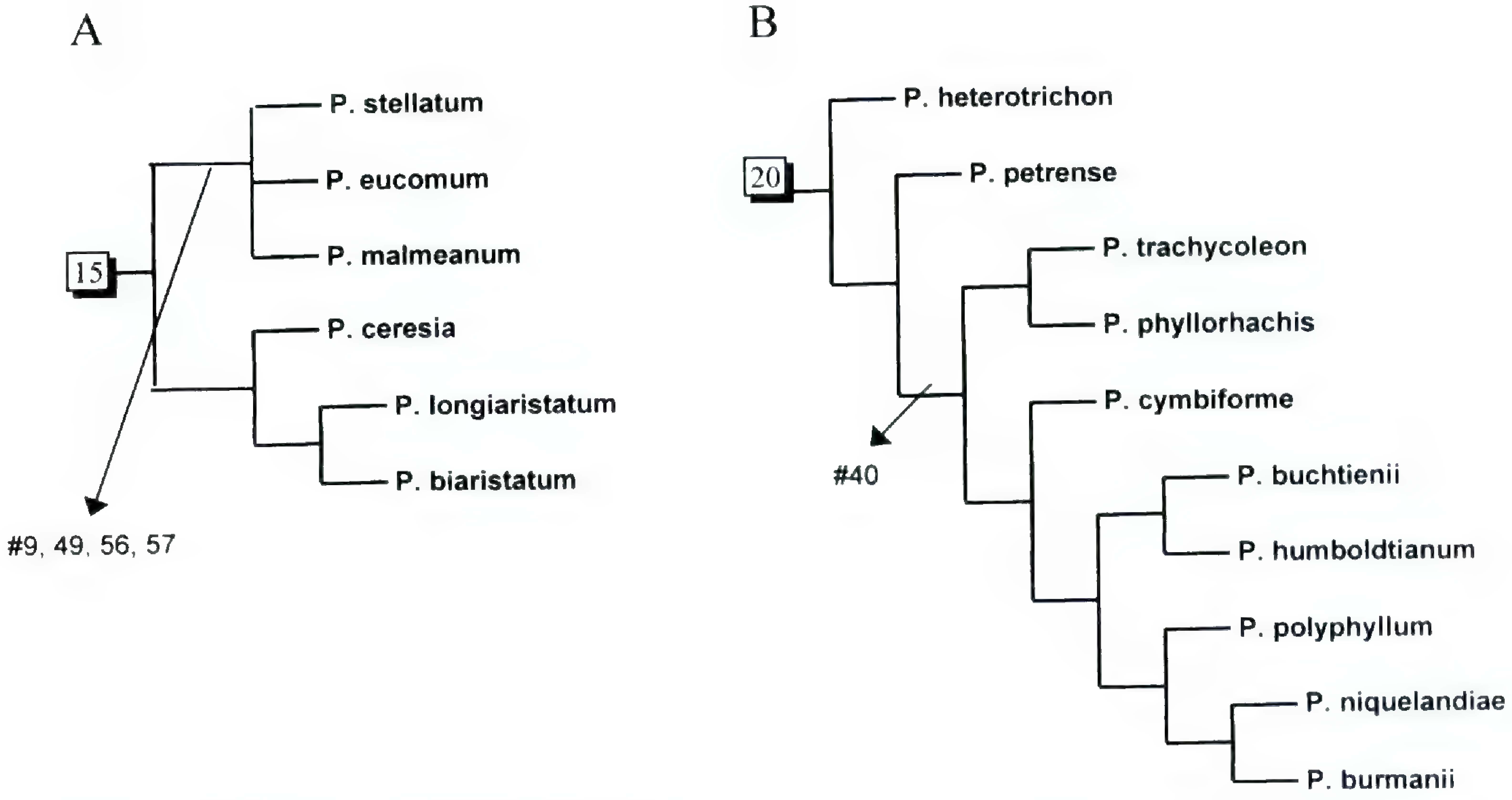

Figure 5. Alternative most parsimonious topologies within *Paspalum* sect. *Ceresia*.—A. Node 15 of cladogram of Figure 4. —B. Node 20 of cladogram of Figure 4.

(presence of approximate racemes); within this section, *P. pectinatum*, *P. cordatum*, *P. imbricatum*, *P. reticulinerve*, and *P. aspidiotes* are grouped together and are very well supported by the presence of characters 19, 20, 27, 30, and 31 (upper glume winged, cordate, 5-nerved, with flat margins, and marginal nerves not reaching the apex) in all of the most parsimonious trees.

The other main clade (see node 7, Fig. 4), including species here considered to be in section *Ceresia*, is supported, in all shortest trees, by characters 24 (upper glume with pilose margins), 26 (upper glume hairy on the lower half), and 30 (margins of the upper glume folded at the nerve). Within this clade, two subgroups (Figs. 3, 4) are recognized: clade A, including *P. goyasense*, *P. carinatum*, *P. eucomum*, *P. malmeanum*, *P. ceresia*, *P. stellatum*, *P. longiaristatum*, and *P. biaristatum*, with the following characters as synapomorphies (node 13, Fig. 4): 42 (lower lemma pilose) and 55 (upper anthecium without silica bodies). In all of the most parsimonious trees, *P. longiaristatum* and *P. biaristatum* constitute a well-supported terminal group (node 19, Fig. 4), both species with an awned upper glume and lower lemma (chars. 21 and 38). Clade B includes *P. heterotrichon*, *P. petrense*, *P. trachycoleon*, *P. phyllorhachis*, *P. cymbiforme*, *P. buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*, and is defined by character 18 (hyaline upper glume) in all trees (node 20, Fig. 4).

Two equally parsimonious topologies were found in clade A: one shown in Figure 4 (node 18), where *P. stellatum* is the sister species of *P. longiaristatum* and *P. biaristatum*, due to support from characters 45 and 46 (lower lemma with marginal nerves and extension of the margins absent). In the other resolution, shown in Figure 5A, *P. stellatum*, *P. eucomum*, and *P. malmeanum* constitute a group supported by characters 9 (two racemes per inflorescence), 49 (obovoid upper anthecium), and 56 and 57 (upper anthecium without macro- and microhairs), with *P. ceresia* as the sister species of *P. longiaristatum* and *P. biaristatum*.

On the other hand, two equally parsimonious topologies were obtained for clade B: in one of them, shown in Figure 4, *P. heterotrichon*, *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis* are monophyletic (node 21), being sustained by characters 13 (spikelets laterally inserted in the pedicels) and 16 (spikelets with an annular thickening at the base). The alternative topology (Fig. 5B) places *P. trachycoleon* and *P. phyllorhachis* as sister group to a clade consisting of *P. cymbiforme*, *P. buchtienii*, *P. humboldtianum*, *P. polyphyllum*, *P. niquelandiae*, and *P. burmanii*. This clade, with eight species, shares a glabrous margin of the lower lemma (char. 40).

Two most parsimonious trees (fit = 413.7 and 199 steps) were obtained using implied weights with PeeWee (trees not included). Regarding the *Paspalum* ingroup, the strict consensus of both trees has the same topology as the tree, obtained with NONA (Fig. 3), where group Racemosa is the sister to subgenus *Ceresia*. Characters supporting clades in the two shortest trees are the same as in the equal weight analysis, except character 24 for section *Ceresia* (node 7, Fig. 4). In both most parsimonious trees

from Pee Wee, groups Eriantha, Dissecta, and Notata are more closely related to each other than to the clade group Racemosa + subgenus *Ceresia.*

Discussion

Monophyly of *Paspalum* subg. *Ceresia* is sustained by the present analysis. Two additional steps are required for breaking down the subgenus *Ceresia* clade, which has a Bremer support of 2 and a jackknife value less than 50; similar low values are common in different cladistic treatments using morphological data (Karis, 1995). Only homoplasic characters support this clade including subgenus *Ceresia*: a membranous upper anthecium (char. 51) is present in nearly all species of the ingroup, but *P. niquelandiae* and *P. goyasense* have a membranous or chartaceous upper anthecium, whereas in *P. ceresia* it is hyaline. Regarding the outgroups, the upper anthecium is membranous in *Anthaenantiopsis fiebrigii,* and membranous to chartaceous in *P. candidum* and *P. cromyorrhizon.* Character 52 (upper palea gaping at the apex, not covered by the upper lemma) is a synapomorphy of the subgenus but also present in *A. fiebrigii.* The winged rachis, widely used to recognize the subgenus, is present in many of the outgroup taxa, evidently arising many times, or being lost, in the evolution of the genus.

Within subgenus *Ceresia* two monophyletic sections are recognized: section **Pectinata**, including *Paspalum lanciflorum, P. cachimboense, P. pectinatum, P. cordatum, P. imbricatum, P. reticulinerve,* and *P. aspidiotes,* and section **Ceresia**, including *P. goyasense, P. carinatum, P. eucomum, P. malmeanum, P. ceresia, P. stellatum, P. longiaristatum, P. biaristatum, P. heterotrichon, P. petrense, P. trachycoleon, P. phyllorhachis, P. cymbiforme, P. buchtienii, P. humboldtianum, P. polyphyllum, P. niquelandiae,* and *P. burmanii.* Section *Pectinata* is weakly supported herein (Bremer support = 1; jackknife value less than 50); a similar delimitation of section *Pectinata* was recently shown by Rua and Aliscioni (in press). Within this section, the group including *P. pectinatum, P. cordatum, P. imbricatum, P. reticulinerve,* and *P. aspidiotes* is well supported (Bremer support = 4; jackknife value = 81), all species sharing a winged and cordate, 5- or more nerved upper glume, with the marginal nerves not reaching the upper third of the glume. *Paspalum lanciflorum* and *P. cachimboense* are basal species within section *Pectinata,* both taxa without a winged and cordate upper glume, but with a lower lemma pilosity similar to other species of section *Pectinata.*

Section *Ceresia* is also weakly supported herein (Bremer support = 1; jackknife value less than 50). Within the section, *Paspalum biaristatum* and *P. longiaristatum* are well-supported sister species (Bremer support = 3; jackknife value = 91) but are not distinct from section *Ceresia.* Therefore, we consider section *Biaristata* (Filgueiras & Davidse, 1994) as included in section *Ceresia,* because retaining section *Biaristata* within our section *Ceresia* will render section *Ceresia* monophyletic.

Taxonomic Treatment

Paspalum subg. **Ceresia** (Persoon) Reichenbach, Consp. Regn. Veg.: 49. 1828. *Ceresia* Pers., Syn. Pl. 1: 85. 1805. *Paspalum* sect. *Ceresia* (Pers.) Nees, Fl. Bras. Enum. Pl. 2: 76. 1829, [as "Paspalus sect. Ceresiae"]. *Paspalum* sect. *Ceresia* (Pers.) Schltdl. ex Müll. Stuttg., Bot. Zeitung (Berlin) 19: 326. 1861, nom. illeg. *Paspalum* subsect. *Ceresia* (Pers.) Benth., Gen. Pl. 3: 1098. 1883. *Paspalum* sect. *Ceresia* (Pers.) Pilg., Repert. Spec. Nov. Regni Veg. 26(15): 230. 1929, nom. illeg. TYPE: *Paspalum ceresia* (Kuntze) Chase [= *Ceresia elegans* Pers.].

Paspalum sect. *Biaristata* Filgueiras & Davidse, Novon 4: 20. 1994. Syn. nov. TYPE: *Paspalum biaristatum* Filg. & Davidse.

Paspalum sect. **Pectinata** Chase ex Rodr.-Rodr., Ernstia 2(1–2): 22. 1992. TYPE: *Paspalum pectinatum* Nees ex Trin.

Plants perennial, erect or leaning on the vegetation. Blades rigid, filiform to lanceolate. Inflorescences with 1 to several racemes, rachis of the racemes winged, hyaline to membranous, 0.8–10 mm wide. Spikelets 1.4–8 mm long, pilose, occasionally glabrous; lower glume absent; lower palea and lower flower absent; upper anthecium pale, hyaline to membranous, chartaceous in some species, the palea free at the apex.

Twenty-five species growing from Mexico to Argentina, Uruguay, and southern Brazil.

Cerea Schltdl., Bot. Zeitung (Berlin) 12: 820. 1854, is a superfluous name for *Ceresia.*

Key to Distinguish the Species of *Paspalum* subg. *Ceresia*

1. Upper glume winged 2
1′. Upper glume not winged 6
2(1). Spikelets glabrous ..... 14. *P. imbricatum*
2′. Spikelets pilose 3
3(2). Spikelets paired, arranged in four series ..... 23. *P. reticulinerve*
3′. Spikelets solitary, arranged in two series 4
4(3). Lower lemma shortly ciliate on the margins, not papillose-pilose ..... 1. *P. aspidiotes*
4′. Lower lemma conspicuously papillose-pilose on the margins 5
5(4). Culms short rhizomatous, 35–100 cm tall; sheaths red or brown, shiny at the outer surface; racemes 2(3 to 5), 2–8 cm long; spike-

lets lanceolate, 5–8 mm long, 2–3.3 mm wide ... 19. *P. pectinatum*

5′. Culms with long, curved rhizomes, 100–130 cm tall; sheaths stramineous or green, not shiny at the outer surface; racemes 5 to 10, 12–16 cm long; spikelets ovoid, 4–5(–6) mm long, 2.5–3.5 mm wide ... 8. *P. cordatum*

6(1). Spikelets with the upper glume and the lower lemma awned ... 7

6′. Spikelets not awned ... 8

7(6). Annual, culms 15–36 cm tall; spikelets 1.8–2.2 mm long; awn of the upper glume 6–12.2 mm long, that of the lower lemma 0.3–2 mm long ... 16. *P. longiaristatum*

7′. Perennial, culms 70–125 cm tall; spikelets 3.8–4.5 mm long; awn of the upper glume 4–7.1 mm long, that of the lower lemma 3.8–4.5 mm long ... 2. *P. biaristatum*

8(6). Rachis (3.5–)4–10 mm wide ... 9

8′. Rachis 1–2.5(–3) mm wide ... 15

9(8). Spikelets solitary ... 10

9′. Spikelets paired ... 13

10(9). Spikelet (4.8–)5.6–7.2 mm long; anthecium ½ to ⅓ length of the spikelet ... 15. *P. lanciflorum*

10′. Spikelet 2.3–3.9 mm long; anthecium as long as or slightly shorter than the spikelet ... 11

11(10). Inflorescences with 1 (rarely 2) racemes, if 2 conjugate; pulvini with 1 or 2 papyraceous bracts; pedicels with a crown of hairs toward the apex; upper anthecium shortly stipitate; blades filiform ... 24. *P. stellatum*

11′. Inflorescences with 1 to 7 alternate racemes; pulvini ebracteate; pedicels hispid, without a crown of hairs toward the apex; upper anthecium not stipitate; blades linear to linear-lanceolate (occasionally filiform in *P. ceresia*) ... 12

12(11). Rachis 3.5–4 mm wide; blades 1.5–4 mm wide; spikelets 2.3–3 mm long, not early deciduous, with an annular thickening at the base; upper glume with papillose-pilose hairs toward the margins, a few of them longer than the rest; lower lemma with long hairs at the upper margins, otherwise glabrous; lodicules 2 ... 12. *P. heterotrichon*

12′. Rachis 6–10 mm wide; blades 3–15(–20) mm wide; spikelets (3–)3.4–3.6 mm long, early deciduous, without an annular thickening at the base; upper glume with ± equal, silky, not papillose-pilose, marginal hairs; lower lemma pilose all over the surface; lodicules absent ... 7. *P. ceresia*

13(9). Plants bambusiform; spikelets glabrous ... 21. *P. phyllorhachis*

13′. Plants herbaceous; spikelets pilose ... 14

14(13). Culms unbranched, 70–90 cm tall; blades 3–6 mm wide; rachis (6.5–)7–7.5 mm wide; upper glume long-acuminate; lower lemma pilose on the lower half, not sulcate ... 20. *P. petrense*

14′. Culms branching, 1–2 m tall; blades 0.5–1.5 cm wide; rachis 4–6 mm wide; upper glume acute to acuminate; lower lemma pilose at the upper portion or glabrous, sulcate ... 25. *P. trachycoleon*

15(8). Annual; upper anthecium long-stipitate ... 5. *P. cachimboense*

15′. Perennial; upper anthecium not stipitate ... 16

16(15). Spikelets solitary; the margins not corky, with hairs up to 3 mm long, appressed or ascendent, irregularly distributed on the margins ... 17

16′. Spikelets paired, occasionally the lower one reduced or aborted; the margins corky, with radiate marginal hairs (ascendent in *P. cymbiforme*) ... 20

17(16). Racemes 2, conjugate; spikelets 1.6–3 mm long, the margins densely pilose on the upper portion, with hairs up to 2 mm long, shortly pilose toward the base; upper anthecium as long as the upper glume and lower lemma ... 18

17′. Racemes 1 to 3, not conjugate; spikelets 3–5 mm long, with long hairs on the basal margins, sparsely and shortly pilose on the upper portion, occasionally glabrous; upper anthecium shorter than the upper glume and lower lemma ... 19

18(17). Spikelets 1.6–2 mm long ... 17. *P. malmeanum*

18′. Spikelets 2.5–3 mm long ... 10. *P. eucomum*

19(17). Racemes 1, occasionally 2; rachis of the branches 1.8–2.5(–3.5) mm wide, straight to subfalcate; upper glume densely pilose on the lower third, otherwise scaberulous; upper glume and lower lemma flat in the upper portion; blades filiform ... 6. *P. carinatum*

19′. Racemes (1)2(3), rachis of the branches 1–1.6 mm wide, straight; lower glume densely pilose in the lower half, otherwise glabrous; upper glume and lower lemma slightly convex; blades linear ... 11. *P. goyasense*

20. Rachis of the branches 2–3 mm wide ... 21

20′. Rachis of the branches 0.8–1.5(–1.8) mm wide ... 22

21(20). Inflorescences 8–12 cm long, with 1 to 4 racemes; floriferous culms 60–90 cm tall; blades linear, 5–19(–24) × 0.2–0.5(–0.8) cm; pseudoligule a ring of hairs ... 9. *P. cymbiforme*

21′. Inflorescences 20–25 cm long, with 9 to 11 racemes; floriferous culms 150 cm tall; blades lanceolate, 30–35 × 1–1.2 cm; pseudoligule absent ... 4. *P. burmanii*

22(20). Plants robust, 120–185 cm tall, blades 20–45 × 0.8–2.2 cm, inflorescences with 8 to 30 racemes ... 18. *P. niquelandiae*

22′. Plants herbaceous, 30–100 cm tall; blades 4–21 cm long, 0.1–1.8 cm wide, inflorescences with 1 to 11 racemes ... 23

23(22). Rachis pilose on one or both surfaces; blades linear to linear-lanceolate, 4–13 cm long, 0.1–0.6 cm wide; upper glume with unequal marginal hairs; lower lemma with ciliate apical margins ... 22. *P. polyphyllum*

23′. Rachis glabrous; blades lanceolate, 5–21 cm long, 0.5–1.8 cm wide; upper glume with marginal hairs evenly distributed, all of the same length; lower lemma with glabrous apical margins ... 24

24(23). Racemes (4)7 to 11, arcuate; rachis of the branches 0.8–1.2(–1.4) mm wide; spikelets 0.8–1(–1.3) mm wide, sparsely distributed; blades papyraceous ... 3. *P. buchtienii*

24′. Racemes 2 to 6, not arcuate; rachis of the

branches 1.2–1.5 mm wide; spikelets 1.2–1.4 mm wide, imbricate; blades herbaceous .... 13. *P. humboldtianum*

1. **Paspalum aspidiotes** Trinius, Sp. Gram. 3: pl. 269. 1829–1830. TYPE: Brazil. Without locality: *G. H. von Langsdorff s.n.* (holotype, LE! photo, SI!; isotypes, P!, US-2942148!). Figures 6, 7.

Paspalum setiglume Chase, Brittonia 3: 150, fig. 1. 1939. Syn. nov. TYPE: Venezuela. Bolívar: Auyan-tepuí, 1100 m, Dic. 1937–Jan. 1938, *G. H. H. Tate 1285* (holotype, NY not seen, photo, K!; isotypes, MO-2704419!, US-1723623! photo, SI!).
Paspalum erectifolium Swallen, Fieldiana, Bot. 28: 22. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, bordering forest of Río Karuai, between Santa Teresita de Kavanayén and base of Ptari-tepuí, 1220 m, 18 Nov. 1944, *J. A. Steyermark 60302* (holotype, US-1911668! photo, SI!; isotypes, MO-3001316!, NY not seen, VEN not seen).

Rhizomatous perennial, with arcuate rhizomes; floriferous culms 30–90 cm tall, 0.3–0.4 cm diam., erect, simple or branched; internodes cylindrical, glabrous, finely striate; nodes compressed, shortly pilose, brown. Sheaths usually longer than the internodes, overlapping, densely villous all over the surface or only at the distal portion, the margins pilose. Ligules membranous, 3–4 mm long, ferruginous, glabrous; pseudoligule a tuft of long white hairs. Blades lanceolate, 8–32 cm long, 0.7–1.5 cm wide, attenuate at the base, the apex acuminate, rigid, ascendent, densely villous on both surfaces, the margins pilose. Terminal inflorescence exserted, subdigitate. Peduncles up to 30 cm long, terete, finely striate, glabrous; main axis up to 4 cm long, flattened, glabrous or sparsely pilose; pulvini pilose; racemes 4 to 7, rarely 3, ascendent, 6–13.5 cm long, alternate; rachis of the racemes flattened, 3–4.5 mm wide, ending in a naked point, shortly pilose, the midnerve manifest, the margins membranous, pale to brown; pedicels short, flat, pilose toward the apex; spikelets solitary, densely imbricate in 2 series. Spikelets broadly ovoid, 6.5–7.5 mm long, 3–4 mm wide, dorsiventrally compressed, pilose, ferruginous, upper glume and lower lemma winged, cordate, the apex rounded. Upper glume papyraceous, 7(–9)-nerved, with 3 central nerves reaching the apex and anastomosed veins between the nerves, with 1 to several white hairs, up to 2.5 mm long, at the apex, the rest of the surface short ciliate, the margins ciliate. Lower lemma glumiform, 5.5 mm long, 3.1 mm wide, papyraceous, 5–7-nerved, corrugate toward the basal portion, ciliate, with one to several white hairs, at the upper margins, otherwise scabrous. Upper anthecium long-ellipsoid, 5 mm long, 1.3 mm wide, shorter than the spikelet, membranous, stramineous, plano-convex, shortly stipitate, minutely papillose, with simple papillae all over the surface, scabrous and with a tuft of macrohairs, bicellular microhairs, and silica bodies at the apex; lodicules 2, conduplicate, hyaline, 0.4 mm long; stamens 3, anthers 1.6 mm long; stigmas 2, plumose, lateral. Caryopsis not seen.

Distribution and habitat. *Paspalum aspidiotes* grows in savannas, on dry and rocky soils, between 100 and 1200 m elevation in Venezuela (Amazonas and Bolívar), Colombia (cited by Judziewicz, 1990), Guyana, Brazil (Amazonas), and Bolivia, where it was recently found in Santa Cruz.

Paspalum aspidiotes is related, within section *Pectinata*, to *P. reticulinerve*, the latter distinguished by paired spikelets. It is also related to *P. cordatum* Hack., a species with spikelets 4–5(–6) mm long, without white hairs on the apex of the upper glume and lower lemma, the upper glume and lower lemma not scabrous over the whole surface, and with conspicuous marginal, tuberculate hairs at the lower lemma.

The study of type material of *P. aspidiotes*, from LE, and that of *P. setiglume*, from K, MO, and US, allowed us to verify that there are no differences between the taxa. There is, within the examined specimens, variation in the number and length of the hairs on the upper margins of the upper glume and lower lemma. Therefore, *Paspalum setiglume* is considered a synonym of *P. aspidiotes*.

The specimen *Riedel s.n.*, collected in Brazil without a definite locality and examined at P, probably represents an isotype of *P. aspidiotes* (see Renvoize, 1978, for comments on *Langsdorff* and *Riedel* collections).

Representative specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff M., *Mostacedo et al. 1862* (LPB). BRAZIL. **Amazonas:** Estrada do Estanho, road to Igarapé Preto, *Calderón et al. 2760* (US); Fortaleza Savanna, Rio Puciari tributary of Rio Ituxi, *Prance et al. 13823* (R, US); Mun. Humaitá, estrada Humaitá–Jacarecanga, km 62, *Texeira et al. 1197* (MO). **Without state:** without locality, *Riedel 1048* (B), *Riedel s.n.* (G, P). GUYANA. Imbaimadai savanna, Upper Mazaruni River, Ayanganna Plateaú, *Fraser 370* (US). VENEZUELA. **Amazonas:** Territorio Federal Amazonas, *Guánchez & Melgueiro 3618* (MO). **Bolívar:** La Gran Sabana, km 145 along hwy., *Davidse 4708* (K, MO, US); Distr. Piar, at top of Salto Aicha near E base of Uaipan-tepui, *Davidse & Huber 22944* (MO); Dist. Roscio, S de Cantarana, *Huber & Alarcón 9643* (MO); Distr. Piar, en las cabeceras nororientales del Río Urimán, *Huber et al. 9898* (MO, US); by first ford W along summit Torom-Meru NW of Parupa, *Kral 72050* (MO).

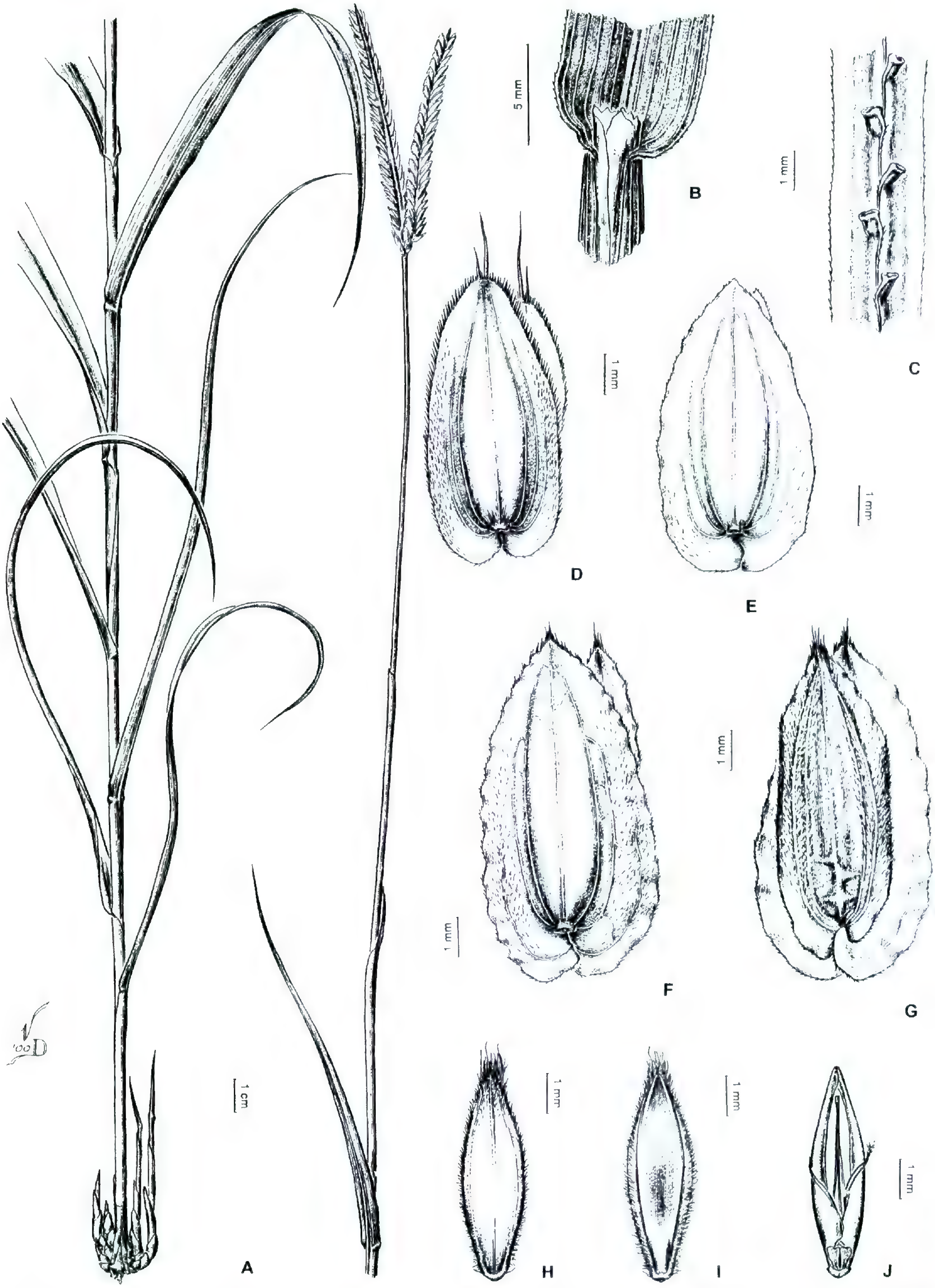

Figure 6. *Paspalum aspidiotes.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D, E, F. Spikelets, upper glume view. —G. Spikelet, lower lemma view. —H. Upper anthecium, dorsal view. —I. Upper anthecium, ventral view. —J. Upper palea, lodicules, and gynoecium. (A–C, E–J based on *Riedel s.n.*, P; D based on *Tate 1285*, US.)

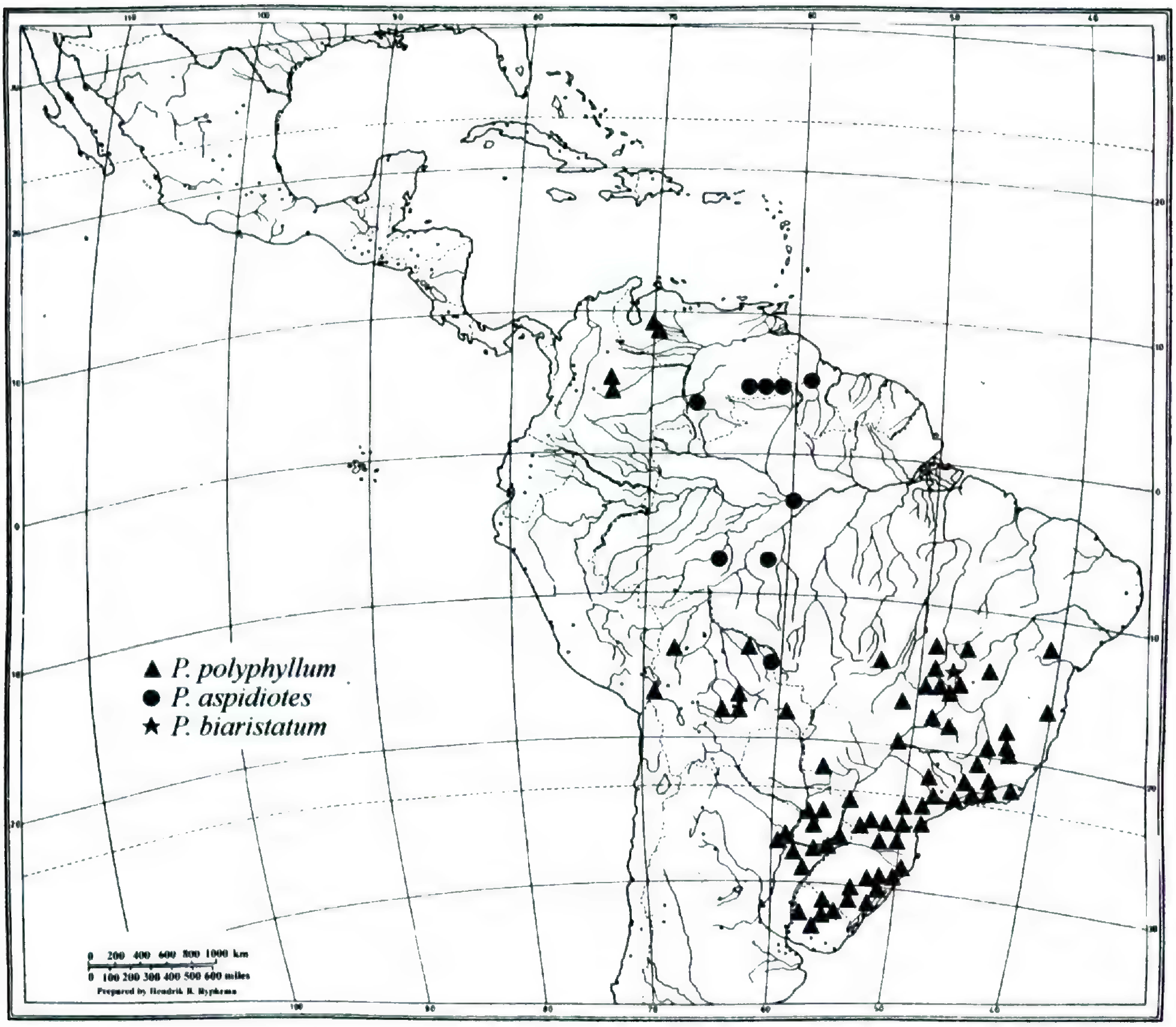

Figure 7. Distribution of *Paspalum aspidiotes*, *P. biaristatum*, and *P. polyphyllum*.

2. Paspalum biaristatum Filgueiras & Davidse, Novon 4: 18, fig. 1. 1994. TYPE: Brazil. Goiás: Niquelândia, Macedo, ca. 14°18'S, 48°23'W, 18 km N de Niquelândia, 10 June 1992, *T. S. Filgueiras 2341* (holotype, IBGE!; isotypes, B not seen, F not seen, FLAS not seen, ICN!, ISC not seen, K! photo, SI!, MEXU not seen, MO!, P not seen, R not seen, RB not seen, SI!, SP not seen, UB not seen, US!). Figure 7.

Caespitose, shortly rhizomatous perennial; culms simple or branched, 70–125 cm tall, 1–1.3 mm diam., rigid; internodes cylindrical, hollow, glabrous; nodes dark, the basal ones glabrous or pilose, the upper ones glabrous. Sheaths 4–7 cm long, shorter than the internodes, keeled, with papillose-pilose hairs, the margins glabrous or ciliate. Ligules membranous-ciliate, the membranous portion 0.2–0.3 mm long, cilia 0.2–0.3 mm long; pseudoligule a ring of hairs 1–1.2 mm long. Blades linear to linear-lanceolate, 7–19 cm long, 0.1–0.9 cm wide, papillose-pilose on both surfaces, attenuated or rounded at the base, the apex long-acuminate, the margins ciliate. Peduncles subexserted or exserted, up to 17 cm long, terete. Terminal inflorescences 6–11 cm long, 3–4 cm wide; main axis absent or up to 6 cm long, glabrous, scabrous; racemes 1 to 4(7), 3–8(–13) cm long, solitary or alternate, distant, arcuate, ending in a naked, acuminate point; pulvini pilose; rachis of the racemes 4.5–7 mm wide, glabrous, with a midnerve prominent and margins membranous, sparsely ciliate; pedicels 0.3–0.5 mm long, solitary, hispidulous; spikelets densely imbricate in two series along the rachis. Spikelets long ellipsoid, awned, 3.8–4.5 mm long without the awn, 0.4–0.5 mm wide, pilose, stramineous to purple. Upper glume hyaline, 3-nerved, densely pilose toward the base, with hairs reaching ½–⅓ the length of the spikelet, otherwise glabrous, the margins densely pilose with hairs 1.7–2.2 mm long; awn 4–7.1 mm long, scabrous. Lower lemma

slightly shorter than the upper glume, membranous, 3-nerved; terminal awn 3.8–4.5 mm long, scabrous. Upper anthecium ellipsoid, 3–3.5 mm long, 0.5 mm wide, shorter than the spikelet, papyraceous, shiny, pilose on the upper portion; upper lemma 5-nerved, the nerves inconspicuous, with bicellular microhairs and macrohairs toward the apex, the margins hairy on the upper third or glabrous, flattened; upper palea with microhairs, macrohairs, hooks, and silica bodies on the distal portion; lodicules absent; stamens 3, anthers 2–2.2 mm long; stigma plumose. Caryopsis 1.2–1.5 mm long, 0.3–0.5 mm wide; hilum punctiform, embryo less than half the length of the caryopsis.

Distribution and habitat. Endemic to central Brazil; it grows in Niquelândia, Goiás, in serpentine soils at 1000 m.

Paspalum biaristatum is related to *P. longiaristatum* by the presence of awned spikelets. The latter is distinguished by its annual habit, spikelets 1.8–2.2 mm long, upper glume with an awn 6–12.2 mm long, and lower lemma with awn 0.3–2 mm long.

Representative specimens. BRAZIL. **Goiás:** Niquelândia, Mun. Niquelândia, Macedo, *Filgueiras & Lopes 2408, 2409* (MO), *Fonseca et al. 224* (MO), *Oliveira et al. 615, 623, 630* (K), *758* (IBGE, SI).

3. Paspalum buchtienii Hackel, Repert. Spec. Nov. Regni Veg. 6: 153. 1908. TYPE: Bolivia. La Paz: Prov. Sud Yungas, Sirupaya a Yanacachi, 2100 m, 1906, *O. Buchtien 420* (holotype, W! photo, K!; isotype, US-2854141! photo, SI!). Figures 8, 9.

Rhizomatous perennial, with leafy, long rhizomes; floriferous culms 60–100 cm tall, ascendent, erect or clambering, rigid, branching at the basal and middle nodes; internodes 5–25 cm long, 0.2–0.3 cm diam., finely striate, glabrous, hollow, stramineous or tinged with purple; nodes compressed, brown, glabrous to shortly pilose. Sheaths 4–15 cm long, the lower ones overlapping, the upper ones shorter than the internodes, glabrous or pilose, the margins membranous, glabrous or ciliate with tuberculate hairs. Ligules membranous, 0.8–1.6 mm long, brown, glabrous; pseudoligule absent. Blades lanceolate, 6–16 cm long, 0.6–1.7 cm wide, flattened, papyraceous, acute at the apex, glabrous to shortly pilose on both surfaces, the margins glabrous or ciliate, shortly pseudopetiolate, pseudopetiole ciliate. Peduncles up to 28 cm long, terete, glabrous. Terminal and axillary inflorescences present, exserted, 10–15 cm long, 6–9 cm wide, truncate; main axis 4–13 cm long, flattened, glabrous; racemes (4)7 to 11, alternate to subopposite, arcuate, the basal ones 6–12 cm long, rachis of the racemes flattened, 0.8–1.2(–1.4) mm wide, keeled and with longitudinal nerves, green to purple, glabrous, the margins scaberulous, ending in a spikelet or in a naked point; pedicels paired, flattened to triquetrous, glabrous, unequal, the upper up to 0.8 mm long; spikelets paired, occasionally the lower one aborted, sparsely arranged in 2 to 4 series. Spikelets long-ellipsoid, 3–3.6 mm long, 0.8–1(–1.3) mm wide, dorsiventrally compressed, acuminate, pilose, pale or tinged with purple. Upper glume hyaline to membranous, 3-nerved, the margins corky, papillose-pilose with radiate, white hairs, otherwise sparsely pilose. Lower lemma glumiform, membranous, 3-nerved, glabrous or shortly and sparsely pilose on the surface, scabrous, with a depression at the base of the dorsal surface. Upper anthecium long-ellipsoid, 2.2–2.6 mm long, 0.8 mm wide, shorter than the spikelet, plano-convex, membranous, stramineous, finely papillose with simple papillae over the surface, scaberulous toward the apex; upper lemma 5-nerved, the margins flat and not covering the apex of the palea, with silica bodies, microhairs, and hooks at the apex; upper palea with microhairs at the apex; lodicules 2, conduplicate, 0.3 mm long; stamens 3, anthers 1.6 mm long; stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. *Paspalum buchtienii* grows in Bolivia (La Paz and Santa Cruz) and Peru (see observations), where it is found on mountain slopes on rocky or limestone soils along forest edges from 460 to 2100 m.

Paspalum buchtienii is closely related to *P. humboldtianum*, a species that is distinguished by its herbaceous leaves, 2 to 6 ascendent, not arcuate, racemes per inflorescence, each raceme (3–)5–9 cm long; the rachis of the racemes is usually 1.2–1.5 mm wide, and the spikelets, 1.2–1.4 mm wide, are imbricate along the racemes.

It was not possible to examine the specimen *Foster & D'Achille 12021* of Parque Nacional Manú, which was cited by Tovar (1993) in his treatment of the grasses of Peru.

The specimens *Steinbach 3015, Beck 8714, 17851*, and *Buchtien s.n.* (K, SI, W) differ by having just 4 to 5 racemes per inflorescence and narrow spikelets, sparsely arranged on the racemes.

Representative specimens. BOLIVIA. **La Paz:** Yungas, *Bang 265* (BM, K, MO, W); Prov. Nor Yungas, Coroico 10 km hacia Coripata, *Beck 8714* (K, MO, SI, US); Prov. Nord Yungas, cerca de 10 km al E de Coroico bajando a Caranavi, *Beck et al. 19948* (K, LPB, SI); Nord Yungas, Polo-Polo bei Coroico, *Buchtien 3629* (MO, US, W); Nord Yun-

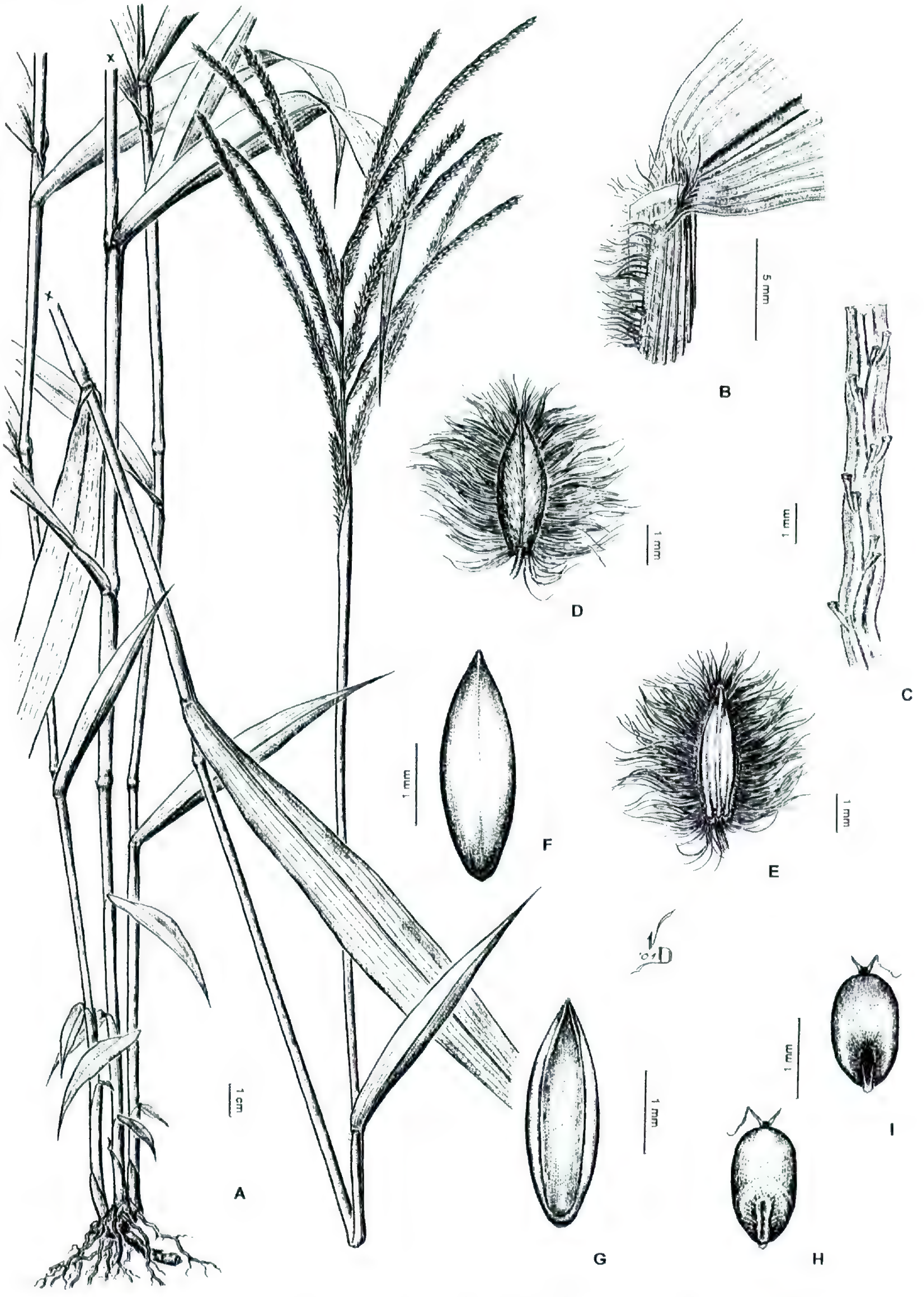

Figure 8. *Paspalum buchtienii.*—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (A, B based on *Beck et al. 19948*, SI; C–I based on *Hollway & Hollway 712*, US.)

Figure 9. Distribution of *Paspalum buchtienii* and *P. carinatum*.

gas, *Buchtien 4274* (BAA, MO); Polo Polo bei Coroico, *Buchtien 447* (B, BM, G, SI); Nord Yungas, *Buchtien s.n.* (K, SI, W). **Santa Cruz:** Prov. A. Ibañez, Quebrada Seca, road to Camiri, *Nee 26848* (MO); Del Para, cerro del Amboró, *Steinbach 3015* (SI).

4. **Paspalum burmanii** Filgueiras, Morrone & Zuloaga, Novon 11: 36, fig. 1. 2001. TYPE: Brazil. Goiás: Mun. Niquelândia, 14°25′S, 48°26′W, margem da estrada entre Niquelândia e Macedo, ca. 10 km N Niquelândia, estrada para Macedo, 20 May 1993, *T. S. Filgueiras 2471* (holotype, IBGE!; isotypes, MO!, SI!, SP!, US!). Figure 10.

Rhizomatous perennials, cataphylls pilose; floriferous culms 1.5 m tall, erect, simple; internodes 12–17 cm long, terete, hollow, lignified, glabrous, smooth; nodes compressed, pilose, brown. Sheaths 15–22 cm long, longer than the internodes, papillose-pilose, with the adaxial surface shiny, the margins shortly pilose. Ligules 2 mm long, membranous, brown; pseudoligule absent, collar pilose. Blades lanceolate, 30–35 cm long, 1–1.2 cm wide, rounded, the apex acuminate, mostly basal, the distal ones small, flat or with involute margins, the basal ones papillose-pilose, midnerve conspicuous. Peduncle subincluded, cylindrical, sparsely pilose. Inflorescences terminal, 20–25 cm long, 5–12 cm wide; main axis 15–20 cm long, glabrous; racemes 9 to 11, ascendent and divergent, alternate, the basal ones 7–9 cm long; pulvini densely pilose with short and long hairs; rachis of the racemes 2.7–3 mm wide, flat, foliaceous, ending in a naked point, occasionally in a spikelet, glabrous, green, the midnerve conspicuous and with anastomosed veins, the margins scabrous; pedicels unequal, terete, scabrous; spikelets paired, imbricate and arranged in 4 series. Spikelets ellipsoid, 3.3–4 mm long, 1–1.2 mm wide, pilose. Upper glume 3-nerved, acuminate, membranous, pilose, more densely so toward the base, the margins corky, hairy, with spreading hairs up to 2 mm long. Lower lemma as long as the

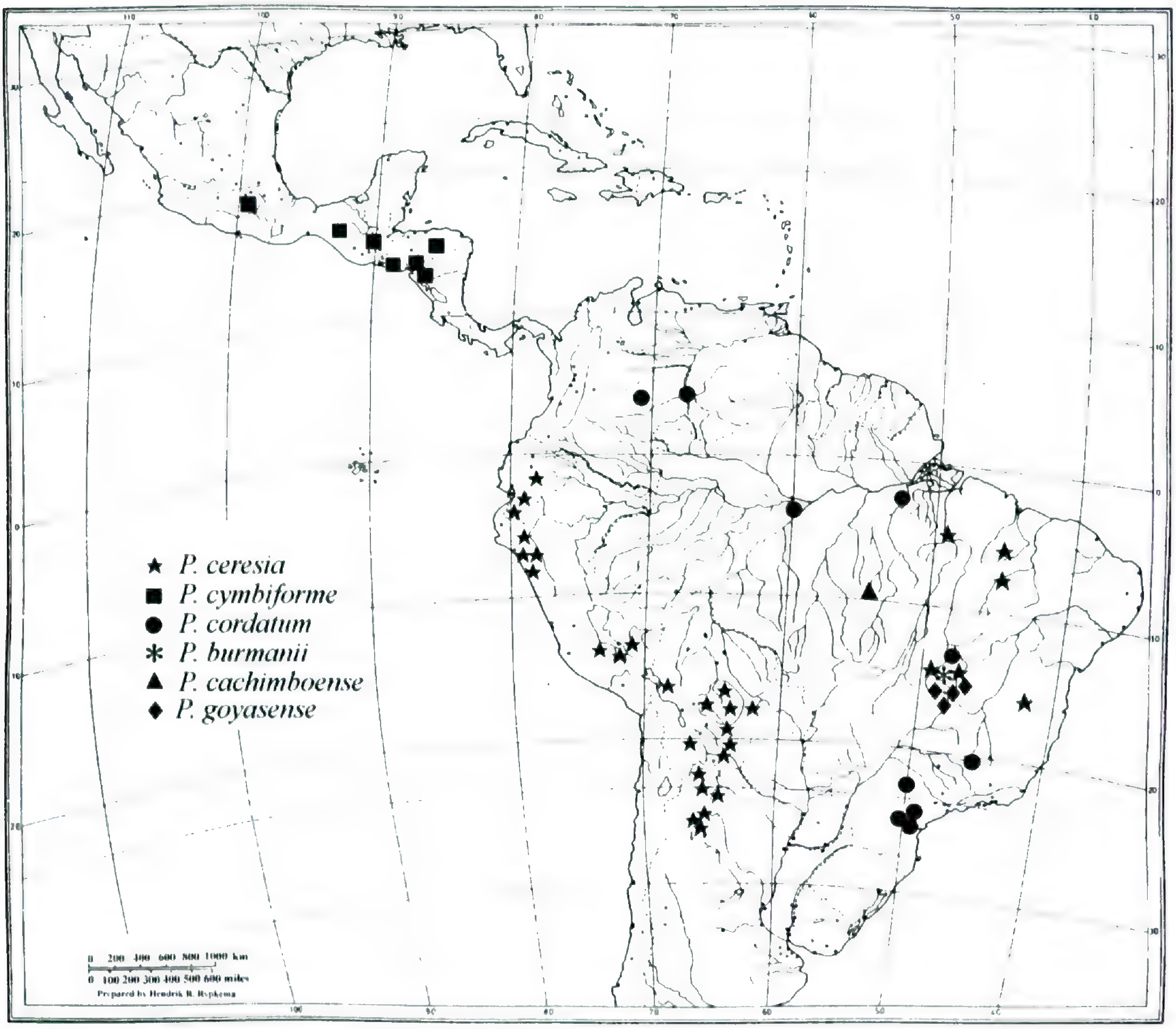

Figure 10. Distribution of *Paspalum burmanii*, *P. cachimboense*, *P. ceresia*, *P. cordatum*, *P. cymbiforme*, and *P. goyasense*.

upper glume, 3–5-nerved, acuminate, membranous, scabrous. Upper anthecium ellipsoid, 3 mm long, 0.8 mm wide, plano-convex, papyraceous, shiny, with simple papillae all over the surface; upper lemma 5-nerved, with silica bodies and prickles on the upper portion, and bicellular microhairs and macrohairs all over the surface; lodicules 2, 0.2 mm long, conduplicate, hyaline; stamens 3, anthers 2 mm long; stigma plumose. Caryopsis obovoid, 1.5 mm long, 0.7 mm wide, brown; hilum punctiform, basal; embryo less than ½ the length of the caryopsis.

Distribution and habitat. Endemic of Niquelândia, in Goiás, central Brazil, on serpentine soils.

Paspalum burmanii is related to *P. niquelandiae*, which can be separated by its spikelets 2.3–3.3 mm long, with the upper glume almost glabrous or shortly hispid on the surface, racemes 8 to 30, rachis of the racemes up to 1.5 mm wide, and pseudoligule a ring of hairs 5–8 mm long. It is also related to *P. humboldtianum*, which differs by its plants 30–100 cm tall, culms branching at the lower and middle nodes, otherwise unbranched, blades 5–21 cm long, 0.5–1.8 cm wide, evenly distributed along the culms, and inflorescences smaller with 2 to 6 racemes, the rachis of the racemes 1.2–1.5 mm wide.

Representative specimen. BRAZIL. **Goiás:** Niquelândia, a 10 km, *Filgueiras 2477* (SI).

5. Paspalum cachimboense Davidse, Morrone & Zuloaga, Novon 11: 389, fig. 1. 2001. TYPE: Brazil. Mato Grosso: Mun. Colider, estrada Santarém–Cuiabá, BR-163, km 762, Serra do Cachimbo a 30 km de Guarantã, 9°35′S, 54°55′W, 19 Apr. 1983, *M. N. Silva, I. L. Amaral, J. Lima, O. P. Monteiro & J. Coêlho 24* (holotype, MO!). Figure 10.

Caespitose annual; floriferous culms 20–70 cm tall, 1.5 cm diam., red-tinged, geniculate, branching at the middle and upper nodes; internodes hollow, glabrous; nodes brown, glabrous. Sheaths 3–8 cm long, usually shorter than the internodes, densely pilose toward the distal portion, otherwise glabrous, the margins membranous. Ligules membranous, 2–3 mm long; pseudoligule absent; collar papillose-pilose. Blades linear to linear-lanceolate, 14–19 cm long, 0.4–0.6 cm wide, attenuate at the base, the apex acute, densely papillose-pilose on both surfaces and along the margins, midnerve manifest. Peduncles exserted, cylindrical, glabrous. Terminal and axillary inflorescences present, 5–8 cm long, 2–5 cm wide; main axis absent; terminal inflorescences with 1 to 4 approximate racemes, axillary inflorescences usually with a single raceme; pulvini pilose, usually with a membranous bract up to 5 mm long; rachis of the racemes winged, 5–8 cm long, 2–3 mm wide, ending in a naked point, glabrous, the midnerve manifest and the margins membranous, nerveless; pedicels flat, glabrous; spikelets solitary, imbricate and arranged in 2 series. Spikelets long-ellipsoid, 4–4.3 mm long, 1–1.1 mm wide, pale, pilose, occasionally glabrous. Upper glume membranous, rounded at the base, the apex acute, 3-nerved, with one central and two submarginal nerves, pilose at the base, the apex shortly ciliate, the rest of the surface glabrous. Lower lemma glumiform, as long as the upper glume, rounded at the base, 3-nerved, the margins with mixed papillose and not papillose hairs, the apex shortly ciliate. Upper anthecium ellipsoid, 2.2–2.5 mm long, 0.8 mm wide, shorter than the spikelet, stipitate, membranous; upper lemma with simple papillae, macrohairs, and bicellular microhairs toward the distal portion; lodicules 2, conduplicate, hyaline; stamens 3, anthers 1.5 mm long; stigmas 2, plumose. Caryopsis not seen.

Distribution and habitat. Endemic to Serra do Cachimbo in central Brazil, where it is known only from the type collection.

Paspalum cachimboense is a member of section *Pectinata* and closely related to *P. lanciflorum*, which differs by its perennial habit, with simple and erect culms, rachis of the racemes (4–)5–7 mm wide, spikelets (4.8–)5.6–7.2 mm long, and upper anthecium 3.2–4.7 mm long.

6. Paspalum carinatum Humboldt & Bonpland ex Flüggé, Gram. Monogr., Paspalum: 65. 1810 [as "Paspalum carinatus"]. TYPE: Colombia. Without locality, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, B-W not seen; isotypes, BM! photo, SI!, US-2942176!). Figure 9.

Paspalum kappleri Hochst. ex Steud., Syn. Pl. Glumac. 1: 21. 1855 [1853]. *Paspalum carinatum* Humb. & Bonpl. ex Flüggé var. *kappleri* (Hochst. ex Steud.) Döll, in Mart., Fl. Bras. 2(2): 96. 1877. TYPE: Surinam. Without locality, 1843, *F. W. Hostmann 1306* (holotype, P!; isotypes, B!, BM!, G!, K! photo, SI!, MO-102047!, P!, US-2855294!, W!).

Paspalum spissum Swallen, Phytologia 14: 358. 1967. Syn. nov. TYPE: Brazil. Maranhão: Carolina to San Antonio de Balsas, 20–25 Mar. 1934, *J. R. Swallen 4050* (holotype, US-1612651! photo, SI!).

Short-rhizomatous perennial; floriferous culms (25–)40–70 cm long, finely striate, glabrous; nodes brown, glabrous to shortly pilose. Sheaths 5–13 cm long, usually shorter than the internodes, glabrous to hirsute, the margins membranous. Ligules membranous, ca. 0.6 mm long, brown, glabrous; pseudoligule absent or present, when present a ring of white hairs. Blades filiform, 5–20 cm long, 0.5–1(–3) mm wide, involute, erect, mostly basal, rounded at the base, the apex setaceous, papillose-pilose on both surfaces, more densely so toward the base of the adaxial surface, the margins involute, ciliate. Peduncles up to 35 cm long, subterete, glabrous. Terminal inflorescences 6–12 cm long, with a membranous bract often at the basal node; main axis absent or up to 3 cm long, flat, glabrous; pulvini glabrous; racemes 1(or 2), alternate when 2 racemes are present, straight or subfalcate, 5–12 cm long; rachis of the racemes winged, 1.8–2.5(–3.5) mm wide, ending in a naked point, glabrous, the midnerve conspicuous, the margins membranous to hyaline, partially covering the spikelets; pedicels short, flat; spikelets solitary, densely imbricate in 2 series. Spikelets long-ellipsoid, 3.3–5 mm long, 1–1.2 mm wide, dorsiventrally compressed, pale, densely pilose at the basal portion, the apex acute or rounded. Upper glume as long as the spikelet, membranous, 3-nerved, densely pilose on the lower portion, with white hairs up to 3 mm long, shortly pilose on the apex, otherwise scabrous. Lower lemma glumiform, slightly shorter than the upper glume, 3-nerved, pilose on the lower portion, the hairs shorter than those of the upper glume, shortly pilose and scabrous at the apex, the rest of the surface glabrous. Upper anthecium long-ellipsoid, 2.7–3.6 mm long, 1 mm wide, 0.6–1.8 mm shorter than the upper glume, plano-convex, flattened toward the distal portion, membranous, shiny, finely papillose with simple papillae all over the surface; upper lemma with macrohairs, bicellular microhairs, and prickles at the upper portion; upper palea with bicellular microhairs and macrohairs at the apex; lodicules 2, 0.2 mm long, conduplicate, hy-

aline; stamens 3, anthers 1.6–1.8 mm long; stigmas 2, plumose, of lateral emergence. Caryopsis ovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic, embryo less than half the length of the caryopsis.

Iconography. Smith et al., Fl. Il. Catarinense: 918, fig. e–g. 1982. Renvoize, The Grasses of Bahia: 214, fig. 79, A. 1984. Judziewicz, Fl. Guianas: 469, fig. 83, D. 1990. Rodríguez, Ernstia 8(2–3): 37. 1998.

Common names. "Grama-das-pedras" (Brazil); "Garcita" (Venezuela); "Pa-mac" (Guyana).

Chromosome number. n = 10 (Davidse & Pohl, 1978); n = 40 (Davidse & Pohl, 1972).

Distribution and habitat. Trinidad and Tobago, Nicaragua, Colombia, Venezuela, Guyana, Surinam, Brazil, and Bolivia. It grows in humid savannas on sandy, rocky, or limestone soils, in open places with periodical fires, between 100 and 1600 m.

Paspalum carinatum is related to *P. goyasense* and *P. stellatum*. *Paspalum goyasense* has inflorescences with two distant racemes, rachis of the racemes 1–1.6 mm wide, ending in a developed spikelet, spikelets with the upper glume densely pilose in the lower half, otherwise glabrous, upper glume and lower lemma slightly convex, and blades linear, 8–20 cm long, 0.2–0.4 cm wide. *Paspalum stellatum* has rachis of the racemes wider [(4–)5–10 mm]; when two racemes are present, they are conjugate, upper glume and lower lemma with long ciliate margins, with hairs up to 4 mm long, and the upper anthecium is 0.4–1 mm shorter than the upper glume and lower lemma.

A rudimentary membranous bract is common in the basal portion of the racemes in *Paspalum carinatum*, as was pointed out by Sendulsky and Burman (1978).

Swallen (1967) related *P. spissum* with *P. carinatum*, characterizing the former by its densely papillose-pilose blades 2–3 mm wide, and appressed to the culms. After examination of many specimens and the type collections, we conclude that there is a notorious variation in these characters: filiform blades are mixed with linear blades in several specimens, such as *Valls & Silva 8340*, *Irwin et al. 27667*, and *Swallen 3687*, *4078*; others have filiform blades with papillose-pilose hairs, e.g., *Davidse & Huber 15436* and *Blydenstein & Saravia 1082*. Therefore, *P. spissum* is here considered a synonym of *P. carinatum*.

Although blades are predominantly basal, cauline blades were present in several specimens. This is probably due to the absence of periodical fires, which are associated with its savanna habitat.

Representative specimens. BOLIVIA. **Beni:** Prov. Vaca Diez, Riberalta, *Beck 20564* (K). **Santa Cruz:** Prov. Velasco, San Ignacio, *Bruderreck 2* (K, LPB, SI); Velasco, 5 km E of Comunidad Carmen del Ruiz, *Killeen 2823* (LPB, MO, US). BRAZIL. **Amapá:** Macapá, *Black & Froés 51–12291* (US); Mun. Calcoene, *Mori & Cardoso 17298* (MO). **Bahia:** 15 km S of intersection of Hwy. BR-020 and Rio Roda Velha, *Davidse et al. 12087* (MO); 51 km E of Barreiras along Hwy. BR-242, *Davidse et al. 12124* (MO). **Distrito Federal:** Brazilandia, *Allem & Vieira 1558* (MO); 31 km from Brasília on Anápolis road, *Clayton 4804* (K, US). **Goiás:** Serra Dourada, ca. 15 km S of Goiás Velho, *Anderson 9969* (COL, K, MO); Barra da Lagoa Formosa, *Glaziou 22547* (G, K, P, W); Formosa, *Glaziou 22556* (K, P, US, W). **Maranhão:** Barra do Corda to Grajahú, *Swallen 3643* (P); Barra do Corda to Grajahú, *Swallen 3687* (US); Carolina a San Antonio de Balsas, *Swallen 4078* (US). **Mato Grosso:** Mun. Amambaí, 12 km E Amambaí-Iguatemi, *Allem & Vieira 2007* (MO); ca. 270 km N of Xavantina, *Ramos & Sousa 182a* (K, US). **Minas Gerais:** Metallurgica, Serra de Ouro Branco, *Chase 10306* (US); Serra do Espinhaço, 8 km E de Diamantina, *Irwin et al. 27667* (MO). **Pará:** Belterra, beira do Lago Jurucuí, *Black 47–1777* (US). **Paraná:** Jaguariaiva, *Dusén 10412* (K); Mun. Ponta Grossa, Vila Velha, *Smith et al. 14462* (K, P, SI, US). **Rio Grande do Norte:** Estremoz to Natal, *Swallen 4762* (US). **Roraima:** along Boa Vista–Bonfim road (BR-401), km 40, *Coradin & Cordeiro 696* (MO). **Santa Catarina:** Rio Capinsel, *Dusén 17934* (K, US). **São Paulo:** Casa Branca, *Chase 10595* (MO, US). **Tocantins:** Ilha do Bananal, Mun. Lagoa da Confusão, Reserva indígena Carajá, *da Silva et al. 4082* (IBGE, SI). COLOMBIA. **Arauca:** Estación de Cravo Norte, *Llano 47* (US). **Boyacá:** Llanos Orientales, al sur de El Yopal, *Blydenstein & Saravia 1082* (COL). **Cundinamarca:** savanna of San Martín, 100 mi. SE of Bogotá, *Shaw s.n.* (US-1343796). **Guaviare:** Mun. San José del Guaviare, serranía La Lindosa, *Giraldo-Cañas & López 2566* (MO). **Meta:** Llanos Orientales, entrada de la Serranía San Martín cerca del río Casibare, *Blydenstein & Saravia 847* (COL). **Vichada:** Territorio Faunístico El Tuparro, entre los ríos Tomo y El Tuparro, El Tapón, *Daniel 60* (COL). GUYANA. Weruni-Ituni savanna, *Abraham 83* (K, US); Rupununi District, Lethem, 4 mi. N of Lethem, *Irwin 739* (US). NICARAGUA. **Zelaya:** ca. 5 km S of Bilwaskarma on road to Puerto Cabezas, *Pohl & Davidse 12274* (MO). TRINIDAD AND TOBAGO. Erin savanna, S of Point Fortin, *Soderstrom 1124* (US). VENEZUELA. **Amazonas:** 3–6 km N de Samariapo sobre ruta a Puerto Ayacucho, *Davidse et al. 16775* (MO). **Anzoátegui:** Distr. Bolívar, just S of El Zamuro, Fila El Purgatorio, *Davidse & González 19317* (MO); Distr. Freites, Burro trail betw. San Durrial & Los Pajaritos, *Davidse & González 19802* (MO). **Apure:** S of San Fernando de Apure, *Alba 53-96* (US). **Bolívar:** Dpto. Heres, margen izquierda de la Quebrada Aguas Negra, 10 km al E del tepuy El Zumbador, *Aynard 6019* (MO). **Guárico:** Estación Biológica Los Llanos, del M. A. C. Calabozo, *Aristeguieta 4219* (MO). **Monagas:** 55 km NWN of San Felix & Rio Orinoco along Hwy. 10 to Maturín, *Davidse et al. 4615a* (MO). **Zulia:** Distr. Perijá, 9 km S of the Machiques intersection along the Maracaibo–La Fria Hwy. (Hwy. 6), *Davidse et al. 18355* (K, MO).

7. Paspalum ceresia (Kuntze) Chase, Contr. U.S. Natl. Herb. 24: 153. 1925. *Paspalum membranaceum* Lam., Tabl. Encycl. 1: 177. 1791, hom. illeg. *Ceresia elegans* Pers., Syn. Pl. 1: 85. 1805. *Ceresia membranacea* (Lam.) P. Beauv., Ess. Agrostogr.: 9 y 171, t. 5, f. 4. 1812. *Paspalum elegans* (Pers.) Roem. & Schult., Syst. Veg. 2: 290. 1817, comb. illeg. *Panicum ceresia* Kuntze, Revis. Gen. Pl. 3: 360. 1898. TYPE: Peru. Without locality, without collector (holotype, P-LA! photo, SI!; isotypes, P!, US-2855815!). Figures 10, 11.

Paspalum membranaceum Lam. var. *aequiglume* Döll, in Mart., Fl. Bras. 2(2): 94. 1877. TYPE: Bolivia. La Paz: Sorata, 2600–2700 m, Feb.–Apr. 1861, *G. Mandon 1255* (lectotype, designated here, W!; isolectotypes, BM!, G!, K!, P!).

Paspalum membranaceum Lam. var. *inaequiglume* Döll, in Mart., Fl. Bras. 2: 94. 1877. TYPE: Brazil. Goiás: campos between Natividade and Conceição, Feb. 1840, *G. Gardner 4029* (lectotype, designated here, B!; isolectotypes, BM!, G!, K!, P!, US-80085!, W!).

Caespitose, short rhizomatous perennial; rhizomes arcuate, covered by pilose cataphylls; floriferous culms 40–80 cm tall, 0.1–0.2 cm diam., branched or unbranched; internodes 4–12 cm long, terete, hollow, glabrous; nodes glabrous. Sheaths 3–12 cm long, glaucous, glabrous to sparsely pilose on the distal portion, the margins membranous, glabrous. Ligules 1–2 mm long, membranous, truncate, glabrous; pseudoligule absent, collar glabrous. Blades filiform, linear-lanceolate or lanceolate, 7–21 cm long, 0.3–1.5(–2) cm wide, flat or with involute margins, rigid, slightly divergent, glaucous, glabrous to sparsely papillose-pilose toward the base of the adaxial surface, the margins glabrous to sparsely papillose-pilose. Peduncles subincluded to exserted, up to 35 cm long, cylindrical, glabrous. Terminal inflorescences exserted, 4–12 cm long, 2–10 cm wide; main axis absent or up to 7 cm long, triquetrous, glabrous; pulvini glabrous or shortly pilose, without papyraceous bracts; racemes (1)2 to 7, ascendent, divergent and alternate, distant; rachis of the racemes 2–7 cm long, 6–10 mm wide, ending in a naked point, glabrous, green or purple at the middle portion, hyaline at the margins, these brown or ferruginous; pedicels up to 0.4 mm long, flat, hispidulous; spikelets solitary and imbricate in 2 series. Spikelets long-ellipsoid, (3–)3.4–3.6 mm long, 1.2–1.4 mm wide, acute, villous, early deciduous; upper glume and lower lemma subequal. Upper glume hyaline to membranous, 3-nerved with one central and two marginal nerves, densely pilose at the base and along the margins, the hairs silky, ascendent, up to 4 mm long. Lower lemma glumiform, hyaline, pilose, with 2 submarginal nerves. Upper anthecium long-ovoid, 2.6–3.6 mm long, 1–1.2 mm wide, not stipitate, hyaline and shiny, white, scabrous and pilose toward the apex; upper lemma with prickles, macrohairs, bicellular microhairs, and silica bodies at the apical portion, upper palea with bicellular microhairs and macrohairs at the apex; lodicules absent; stamens 3, anthers 2.4–2.8 mm long. Caryopsis obovoid, 1.2–1.6 mm long, 0.8 mm wide; hilum punctiform, embryo ½ the length of the caryopsis.

Distribution and habitat. Ecuador, Peru, Brazil, Paraguay, Bolivia, and Argentina, in rocky mountain slopes and open fields on sandy and rocky soils, between 300 and 3000 m.

Paspalum ceresia is related to *P. stellatum*, a species with filiform leaves 8–27 cm long, 0.1–0.3 cm wide, 1 (occasionally 2) racemes, 1 or 2 papyraceous bracts in the basal pulvini, radiate hairs on the pedicels, lodicules present, and upper anthecium stipitate. *Paspalum ceresia* is also similar to *P. trachycoleon*, a species from Central America, Venezuela, Colombia, and southern Brazil, which is characterized by the rachis of the racemes 4–6 mm wide, spikelets paired, with an annular thickening at the base, and lower lemma membranous, 3-nerved.

A single collection was examined from Paraguay, *Isabell s.n.* at P, a specimen without any information about collection date or locality; it is possible this specimen was mislabeled, considering the distribution range of the species.

There is considerable variation in the leaf shape, from filiform to linear and rigid, up to 0.3 cm wide, in the specimens *Oliveira et al. 305, 598, Pinheiro & Carvalho 142, 517, 625, Gardner 4029, Brooks et al. 125, Eiten & Eiten 4418, 3777, 10789,* and *Swallen 3772*, filiform and lanceolate in a single specimen, e.g., *Souza et al. 5548, Filgueiras 2280,* or with lanceolate leaves, up to 2 cm wide, as in *Vee 40372.*

Doell (1877) described variety *aequiglume* and variety *inaequiglume* of *P. membranaceum* on the basis of variation of the upper glume and lower lemma length, a variable character according the degree of maturity of the spikelets. This author cited the specimens *Rhodé s.n.* and *Mandon 1255* as syntypes of variety *aequiglume*, of which *Mandon 1255* agrees with the protologue and is here selected as lectotype of this taxon. Also, Doell (1877) cited *Pohl s.n.* and *Gardner 4029* as syntypes of variety *inaequiglume*, of which *Gardner 4029* is here chosen as lectotype of the variety.

Figure 11. *Paspalum ceresia*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper lemma. —I. Caryopsis, scutellar view. —J. Caryopsis, hilum view. (A–H based on *Hunziker et al. 10354*, SI; I, J based on *Cabrera et al. 22135*, SI.)

Representative specimens. ARGENTINA. **Jujuy:** Dpto. Santa Bárbara, El Fuerte, *Cabrera & Fabris 22730* (US); Dpto. Humahuaca, Sierra de Zenta, *Venturi 8320* (K, LIL, MO, P, SI, W). **Salta:** Dpto. Candelaria, Unquillo, *Schreiter 9256* (LIL); Dpto. Guachipas, Alemanía, *Venturi 9905* (MO, W). **Tucumán:** San Pedro de Colalao, *Dinelli 12876* (LIL). BOLIVIA. **Chuquisaca:** 15 km S of Padilla, *Renvoize & Cope 3870* (K, MO). **Cochabamba:** Prov. Quillacollo, ca. 45 km hacia Oruro, *Beck 4025* (US). **Potosí:** Prov. Charcas, Qda. Llama Chaqui, *Mostacedo 314* (MO). **Santa Cruz:** Prov. Caballero, 15 km arriba de San Juan de Portero, *Killeen & Vargas 4152* (MO); Prov. Florida of Río Mairana, 3 km N of hwy. at Yerba Buena, *Nee 40372* (K, MO). **Tarija:** Tarija, *Fiebrig 2664* (SI). BRAZIL. **Goiás:** Faz. Buracão, ca. 35 km (by road) N of Goianésia, *Brooks et al. 125* (K, MO, NY); Niquelândia, ca. 18 km W de Niquelândia, *Filgueiras 2280* (MO, US); Niquelândia, 2 km da estrada de Chao para o Macedo Velho, *Oliveira et al. 305* (SI); Mun. Niquelândia, Macedo, ca. 0.1 km abaixo da mina de niquel, *Oliveira et al. 598* (US). **Maranhão:** Mun. Lorêto, Ilha de Balsas region, *Eiten & Eiten 3777* (K, US), *4418* (K); Barra do Corda to Grajahú, *Swallen 3772* (K, P). **Minas Gerais:** Retiro ca. 16 km da cidade em direção a Mato Verde, *Souza et al. 5548* (K). **Pará:** Estreito-Marabá, km 1, 4 Abr. 1974, *Pinheiro & Carvalho 142* (US); km 2, *Pinheiro & Carvalho 517, 625* (US). ECUADOR. **Azuay:** valley of the Río Paute, between Paute and Cuenca, between Ríos Azogues & Gualaceo, *Camp 2332* (K, P, US, W). **Loja:** road San Pedro de la Bendita (W of Catamayo)–El Cisne, *Øllgaard et al. 90721* (MO); 6 km W of Colaisaca on road to Sozoranga, *Peterson & Judziewicz 9478* (K, MO, US). PARAGUAY. **Without department:** without locality, *Isabell s.n.* (P). PERU. **Apurimac:** Prov. Abancay, Cunyac, *Chávez 3217* (MO). **Cajamarca:** Prov. Chota, El Tingo, a 6 km sobre la carretera Cochabamba–Huambos, *Sánchez Vega 2332* (SI, US); Dpto. Cajamarca, 4 km E of Celendin on road to Balsas, *Hutchinson & Wright 5194* (G, K, MO). **Cuzco:** Prov. Anta, Mollepata, *Vargas 19047* (MA). **Huancavelica:** entre Izcuchaca y Acoria, *Tovar 1020* (US).

8. Paspalum cordatum Hackel, Ark. Bot. 9(15): 5. 1910. TYPE: Brazil. Paraná: Rio Tibagy in der Nähe des Städtchens Ponta Grossa, am Rande eines Sumpfes, 7 Ene. 1904, *P. K. H. Dusén 3248* (holotype, W!; isotypes, G!, US-2942131!). Figures 10, 12.

Robust, rhizomatous perennials with long, arcuate rhizomes; floriferous culms erect, 100–130 cm tall, 0.4–1 cm diam., unbranched; internodes finely striate, hollow, glabrous; nodes compressed, glabrous, brown. Sheaths usually longer than the internodes, the lower ones overlapping, loose, densely hirsute on the basal portion or glabrous, the inner surface shiny, brown to red-tinged, the margins membranous. Ligules membranous, 1–1.3 mm long, brown, glabrous; pseudoligule a ring of dense, rigid hairs up to 6 mm long; collar densely pilose. Blades linear, 10–50 cm long, 0.5–1.1 cm wide, flat, the margins involute, ascendent and rigid, densely villous on both surfaces, attenuated at the base, the apex beaked. Peduncles exserted, up to 45 cm long, subterete, glabrous. Terminal inflorescences exserted, 7–18 cm long, 6–18 cm wide, subdigitate; main axis up to 4 cm long, wavy, glabrous to sparsely pilose; pulvini pilose; racemes 5 to 10, 12–16 cm long, ascendent, alternate to subopposite, ending in a naked point; rachis of the racemes flat, 1.8–2.4 (–3.2) mm wide, glabrous and green, the margins shortly winged, scaberulous; pedicels short, glabrous; spikelets solitary, densely imbricate in 2 series. Spikelets ovoid, 4–5(–6) mm long, 2.5–3.5 mm wide, dorsiventrally compressed, pale, winged, cordate, the apex acute. Upper glume as long as the spikelet, membranous, glabrous, cordate, 5-nerved, with 3 central nerves reaching the apex, and 2 lateral nerves only notorious at the base. Lower lemma 3.4–3.6(–5) mm long, 1 mm wide, subcordate, 3-nerved, the margins with rigid and thick papillose-pilose hairs, not winged, shortly pilose. Upper anthecium ellipsoid, membranous, 3–3.2 mm long, 0.8 mm wide, shorter than the spikelet, plano-convex, pilose on the upper margins, pale; upper lemma with simple papillae all over the surface, and bicellular microhairs, macrohairs, and silica bodies toward the apex; upper palea with simple papillae, bicellular microhairs, and macrohairs on the upper portion; lodicules 2, ca. 0.4 mm long, conduplicate, hyaline, glabrous; stamens 3, anthers 1.6 mm long; styles 2, stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. This species grows in southern Brazil, in the states of Amazonas, Paraná, Goiás, Minas Gerais, and São Paulo, also in Colombia, in the states of Meta and Vichada, in open areas, lowlands, and swamps.

Rodríguez (1998) considered *Paspalum cordatum* as a synonym of *P. pectinatum* without indicating the criteria for such a decision. Both species share spikelets with the upper lemma not winged and with conspicuous rigid, papillose-pilose hairs on the margins. Nevertheless, we consider *P. pectinatum* a different entity by including specimens with 2, occasionally 3, conjugate racemes, 2–8 cm long, per inflorescence. Additionally, plants, which grow in savannas or open fields on sandy or rocky soils, are smaller and more densely caespitose than those of *P. cordatum*, with lower sheaths burnt by fire.

Paspalum cordatum is also related to *P. imbricatum*, this species with glabrous spikelets and lower lemma winged.

Note that in the specimens *Blydenstein 939* and *Cabrera 2278*, the rachis of the racemes is 3–3.2 mm wide, with crenate margins, and spikelets are bigger, 5.2–6 mm long.

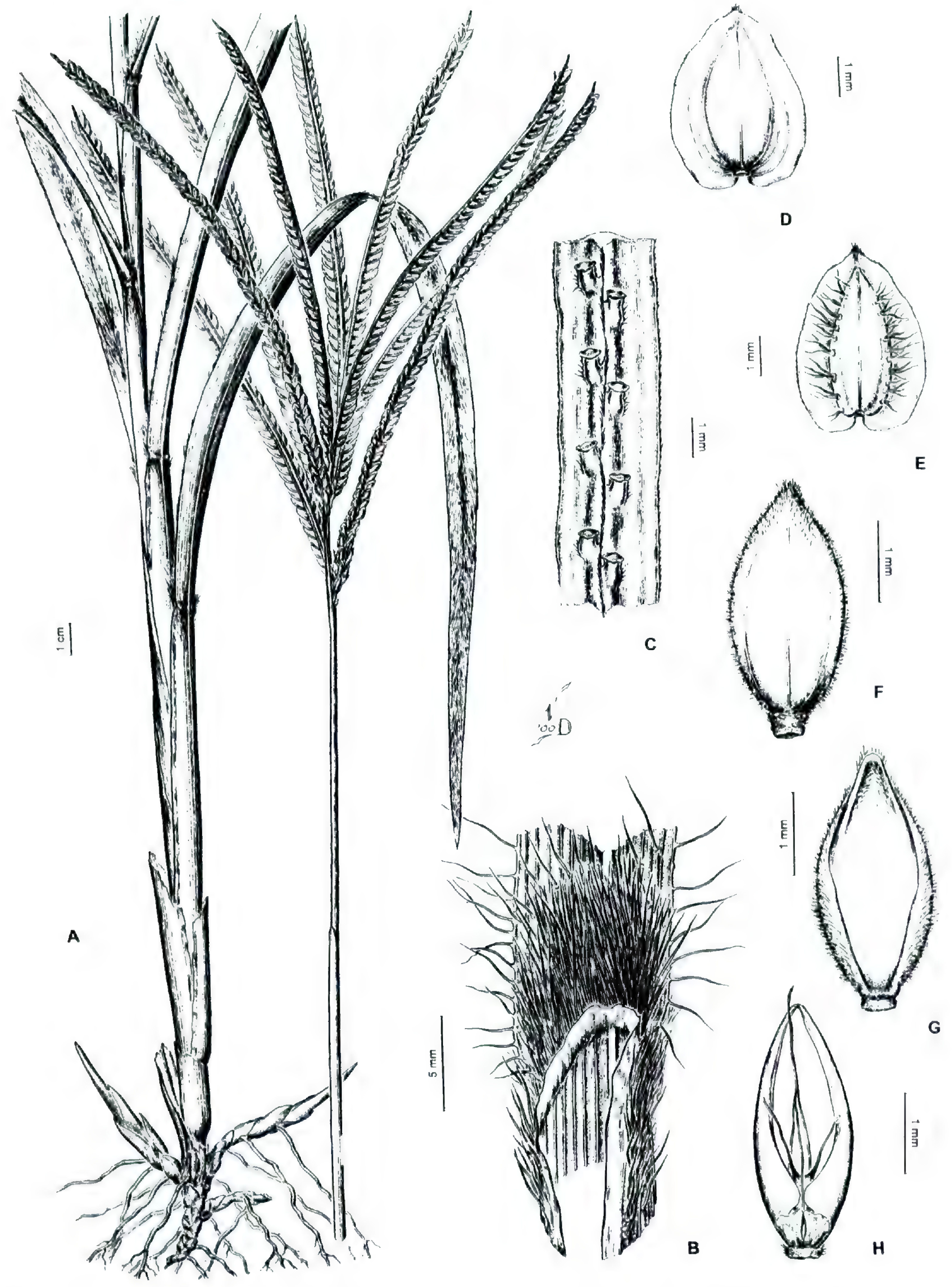

Figure 12. *Paspalum cordatum*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper lemma, lodicules, and gynoecium. (Based on *Hatschbach & Renvoize 5276*, US.)

Representative specimens. BRAZIL. **Amazonas:** Transamazon Hwy., 53 km W de Aripuana River, *Calderón et al. 2708* (MO, US-3082134). **Goiás:** Jataí, *Macedo 1543* (US). **Minas Gerais:** without locality, *Weddell 1699* (G, P). **Paraná:** Turma, in paludosis, *Dusén 9109* (BM, US); Jaguariaiva, *Dusén 16174* (BM, G, SI, US); Mun. Campo Largo, Serra S. Luis, *Hatschbach et al. 12097* (K, MBM); Mun. Pirai do Sul, Serra das Furnas, *Smith et al. 14579* (K, P, SI, US); Mun. Senges, Faz. Morungava, Rio Funil, *Smith et al. 14858* (K, P, US); Ponta Grossa, Faz. Cambujan, *Brade 19638* (US). **São Paulo:** Estação Florestal de Paraguaçu Paulista, 6 km N of city, *Clayton 4631* (K, US). COLOMBIA. **Meta:** Llanos orientales, Hato Pozones, *Blydenstein 939* (COL, MO). **Vichada:** Caño Urimica, *Cabrera 2278* (COL).

9. Paspalum cymbiforme E. Fournier, Mexic. Pl. 2: 5. 1886. TYPE: Mexico. México: San Pablo, *F. M. Liebmann 226* (lectotype, designated by Chase (1929: 20), C not seen). Figure 10.

Shortly rhizomatous perennial; floriferous culms 60–90 cm tall, branching at the middle nodes or simple; internodes terete, striate, glabrous; nodes brown, covered by ascendent white hairs. Sheaths longer than the internodes, striate, glabrous, the margins ciliate at the lower portion. Ligules brown, membranous, 1–1.2 mm long; pseudoligule a ring of hairs. Blades linear, 5–19(–24) cm long, 0.2–0.5(–0.8) cm wide, flat, glabrous or shortly pilose on the adaxial surface, the margins with tuberculate hairs up to 5 mm long, shortly pseudopetiolate, pseudopetiole with short, white hairs. Peduncles exserted, 15–20 cm long, terete, pilose. Terminal inflorescences 8–12 cm long, 3–4 cm wide; main axis absent or up to 5 cm long, shortly hispid or glabrous; pulvini pilose; racemes 1 to 4, 3–8 cm long, alternate, ending in a naked point; rachis of the racemes 2–2.8 mm wide, green and tinged with purple, the midnerve manifest, wings short, hyaline, nerveless; pedicels ca. 0.3 mm long, pubescent, spikelets paired and imbricate in 2–4 series, usually the lower spikelet aborted. Spikelets long-ellipsoid, 3 mm long, 1 mm wide, acute, pilose, pale. Upper glume hyaline to membranous, 3-nerved, with one central and two submarginal conspicuous nerves, the margins corky, with long, ± ascendent hairs, up to 3 mm long, and with small hairs on the basal portion. Lower lemma as long as the upper glume, membranous, 3-nerved, shortly pilose toward the apex, otherwise glabrous, depressed on the basal portion. Upper anthecium long-ellipsoid, 2.2 mm long, 0.8 mm wide, pale, membranous; upper lemma 3-nerved, finely papillose and with prickles, silica bodies, and bicellular microhairs at the apex; upper palea papillose, with macrohairs and bicellular microhairs at the apex; lodicules 2, 0.2–0.3 mm long, conduplicate, hyaline; stamens 3, anthers 1.5 mm long; stigma plumose, lateral. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 21, fig. 4. 1929.

Distribution and habitat. Found from southern Mexico to Nicaragua, on mountain slopes on rocky soils, between 750 and 1300 m.

This species differs from *P. humboldtianum* and *P. polyphyllum* by the rachis 2–2.8 mm wide (vs. 1.2–1.5 mm in *P. humboldtianum* and 1–1.2 mm in *P. polyphyllum*), and by the presence of hairs at the apical portion of the lower lemma.

The specimen *Davidse et al. 31637* has 2 to 7 racemes per inflorescence.

Representative specimens. EL SALVADOR. **La Libertad:** *Eggler 639* (US). **Santa Ana:** Mun. Candelaria de la Frontera, Cerro El Yupe, *Linares 3663* (MEXU). GUATEMALA. **Zacapa:** lower slopes of Sierra de las Minas, along trail above Río Hondo, *Steyermark 29550* (US). HONDURAS. **Distrito Federal:** Llamapa, SW of Talanga, Rancho Santa Regina de Archaga, *Pohl & Gabel 13531* (MO). **Francisco Morazán:** 26 km N of Pespire along Hwy. 1 to Tegucigalpa, *Davidse & Pilz 31637* (MO); region of Las Mesas, *Swallen 10809* (MO, US), *10747* (US). **Olancho:** El Espino, 8 km NE de Catacamas, *Enamorado 23* (MO). MEXICO. Consoquitla, *Liebmann 225* (MO); Mun. Frontera Comalapa, 6–8 km E of Frontera Comalapa along road to Ciudad Cuauhtemoc, *Breedlove 39106* (MEXU). **Chiapas:** Mun. Ixtapa, along Mexican Hwy. 190 in the Zinacantán Paraje of Muctajoc, *Breedlove 13822* (MEXU, US). **Mexico:** Temascaltepec, Bejucos, *Hinton 2532* (BAA, K). NICARAGUA. **Chinandega:** Volcán Casita, Montaña del Cielo, 12°42′N, 86°58′W, *Rueda & Aller 1200* (MO).

10. Paspalum eucomum Nees ex Trinius, Sp. Gram. 1: pl. 110. 1828. *Paspalum eucomum* Nees, Fl. Bras. Enum. Pl. 2: 37. 1829, hom. illeg. TYPE: Brazil. Without locality, *F. Sellow s.n.* (holotype, LE not seen; isotypes, BM!, K! photo, SI!, P!, US-2854694!, US-2854695!). Figures 13, 14.

Paspalum eucomum Nees ex Trin. var. *pilosior* Döll, in Mart., Fl. Bras. 2(2): 65. 1877. TYPE: Brazil. Minas Gerais: Lagoa Santa, *E. Warming s.n.* (holotype, not located; isotype, US-2854696!).

Paspalum splendens Hack., Oesterr. Bot. Z. 51: 238. 1901. TYPE: Brazil. Goiás: without locality, *A. F. M. Glaziou 22554* (lectotype, designated here, W!).

Caespitose, shortly rhizomatous perennial; floriferous culms 60–110 cm tall, 0.2–0.3 cm diam., erect, ascendent, unbranched, occasionally branching at the middle nodes; internodes 6–15 cm long, striate, glabrous; nodes glabrous. Sheaths usually longer than the internodes, 8–25 cm long, overlapping, glabrous or papillose-pilose all over the sur-

Figure 13. *Paspalum eucomum*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and anthers. (Based on *Chase 9097*, US.)

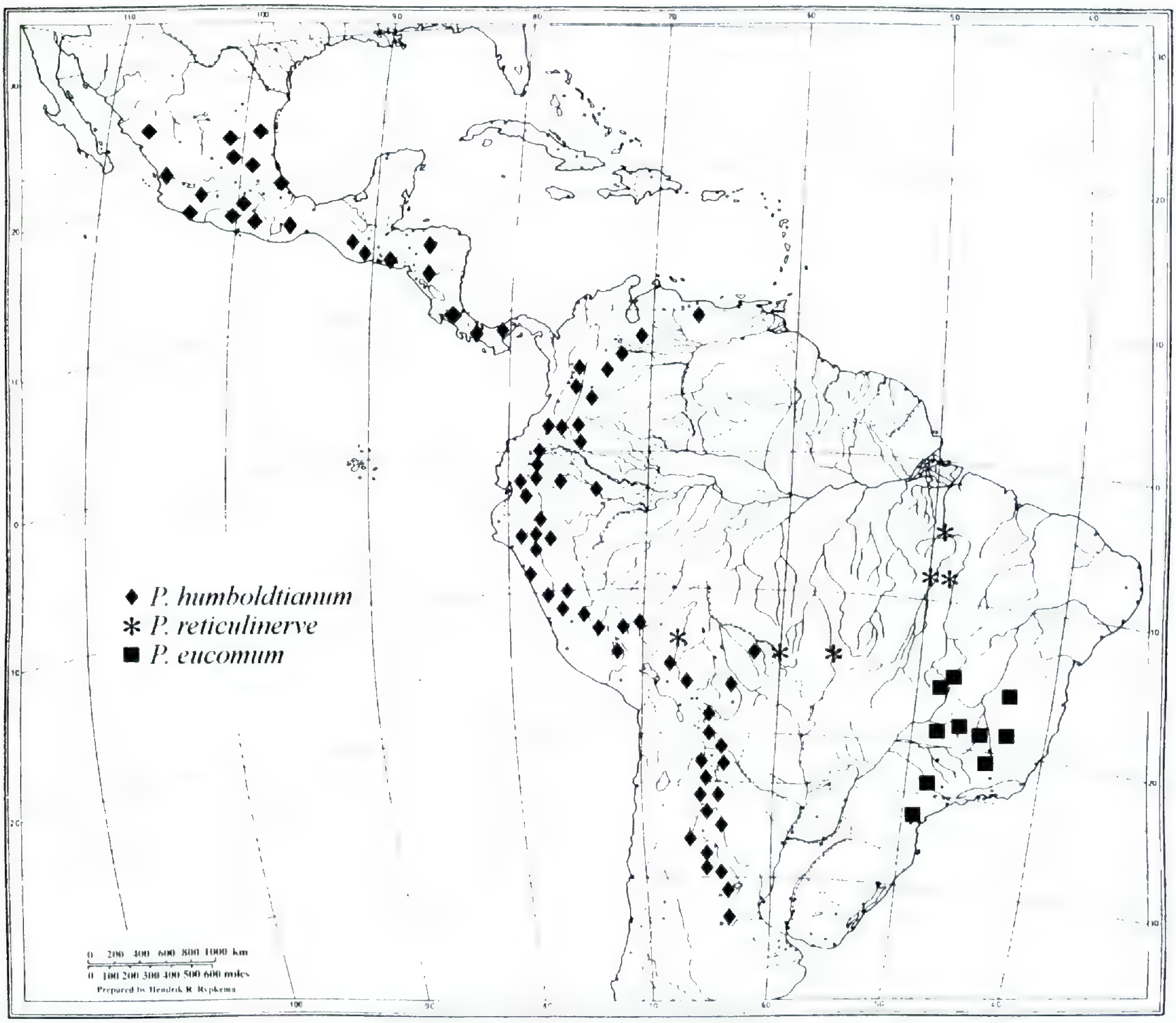

Figure 14. Distribution of *Paspalum eucomum*, *P. humboldtianum*, and *P. reticulinerve*.

face or only at the distal portion, the hairs up to 5 mm long, the margins membranous, glabrous or with one margin ciliate. Ligules membranous, 0.2–0.5 mm long, truncate, brown, glabrous; pseudoligule a ring of white hairs up to 2.5 mm long. Blades filiform, 10–30 cm long, 0.2–0.5 cm wide, erect or flexuous, rigid and involute, narrow, the apex setaceous, adaxial surface with conspicuous papillae and tuberculate hairs, abaxial surface glabrous or both surfaces densely hirsute. Peduncles exserted, up to 30 cm long, subterete, pale or purple, glabrous. Terminal inflorescences conjugate; main axis absent; pulvini pilose, with a bract usually present; racemes 2, (4–)6–17 cm long, occasionally with a third approximate raceme, ascendent, divergent, ending in a naked point; rachis of the racemes 1.5–2.5(–4) mm wide, shortly winged, glabrous, green to purple, the margins hyaline, nerveless; pedicels short, flat, and sparsely pilose; spikelets solitary, densely imbricate in 2 series. Spikelets ellipsoid, 2.5–3 mm long, 1.4–1.6 mm wide, dorsiventrally compressed, acute, densely pilose toward the base and the margins, pale or tinged with purple. Upper glume as long as the spikelet, membranous, 3-nerved, the base and margins covered with white, rigid hairs, the rest of the surface with short and appressed hairs. Lower lemma glumiform, slightly shorter than the upper glume, 3-nerved. Upper anthecium obovoid, 2.4–3 mm long, 1.2 mm wide, membranous, pale, shiny, rounded at the apex, smooth; lodicules 2, ca. 0.3 mm long, membranous, conduplicate; stamens 3, anthers 1.5 mm long; stigma plumose, lateral. Caryopsis not seen.

Distribution and habitat. Restricted to central and southern Brazil in the states of Goiás, Minas Gerais, São Paulo, Paraná, and in the Federal District. It grows in cerrados, in open fields on sandy soils, between 700 and 1100 m.

Paspalum eucomum is closely related to *P. mal-*

meanum. The latter species mainly differs by the spikelets 1.6–2 mm (vs. 2.5–3 mm long); also, *P. malmeanum* grows in Bolivia and Mato Grosso, on flooded soils, while *P. eucomum* occurs in central and southern Brazil, usually in drier settings. It should be pointed out that spikelet size, 2.3–2.5 mm long, is intermediate between both species in *Macedo 351, Sendulsky 1239,* and *Glaziou 17406.* These species are here considered as different entities until more material becomes available.

Chase (ined.) distinguished *P. eucomum* from *P. splendens* by the spikelet size (2.5 mm long vs. 3 mm), rachis width (1.5–2 mm vs. 2–3.5 mm), and general aspect of plants (delicate vs. robust). Upon study of many specimens, we conclude that there is a gradation in these characters, which are not useful to distinguish both species.

Chase (ined.) and Sendulsky and Burman (1980) pointed out that *Glaziou 22555* is one of the syntypes of *Paspalum splendens.* Nevertheless, Hackel (1901) cited, as syntypes, the specimens *Glaziou 22552, 22553,* and *22554,* of which *Glaziou 22554* agrees with the original diagnosis and is here designated as lectotype of the species.

The rachis of the racemes is exceptionally wide, up to 4 mm, in the specimens *Dias et al. 67* and *Weddell 2556.*

Chase (ined.) studied, at B, two specimens collected by *Sellow, 1238* and *1336,* which were examined by Nees and probably represent isotypes of *P. eucomum.* Duplicates of these collections from US were identified by us as *P. eucomum.*

Representative specimens. BRAZIL. **Distrito Federal:** Brasília, *de Jesus 3* (US); Brasília, *Dias et al. 67* (MO); E margin of Lagoa Paranoá, *Irwin et al. 15328* (K, MO, US). **Goiás:** without locality, *Glaziou 22551* (B, G, K, P), *Glaziou 22555* (K, MO, P, US). **Minas Gerais:** between Sucupira and Omega, S of Uberlandia (Uberabinha), *Chase 11200* (BM, K, US, W); Serra de S. José, *Glaziou 17406* (P, US, W); without locality, *Macedo 351* (US); Conceição do Mato Dentro, Rodovia Belho Horizonte, 10 km antes de Chapéu do Sol, *Sendulsky 1239* (US). **Paraná:** Porto Amazonas, *Dusén 18065* (BM, MA, MO, P, SI). **São Paulo:** Mun. Botucatú, 18 km N of Botucatú, 14 km E of São Manuel, *Gottsberger 1043* (US). **Without state:** without locality, 1844, *Weddell 2556* (P).

11. Paspalum goyasense Davidse, Morrone & Zuloaga, Novon 11: 391, fig. 2. 2001. TYPE: Brazil. Goiás: 25 km E de Cabeceiras (ca. 4 km E of Goiás–Minas Gerais), cerrado, 1000 m, 19 Nov. 1965, *H. S. Irwin, R. Souza & R. Reis dos Santos 10524* (holotype, MO!; isotype, US-2529124!). Figure 10.

Caespitose perennial; culms 40–65 cm tall, erect, unbranched, few-noded; internodes 2–3, 6–20 cm long, 0.1 cm diam., terete, hollow, glabrous; nodes brown, densely pilose. Sheaths 3–10 cm long, mostly basal, papillose-pilose or hispid, the margins membranous. Ligules 0.5–0.9 mm long, membranous, brown, glabrous; pseudoligule absent; collar pilose. Blades linear, 8–20 cm long, 0.2–0.4 cm wide, mostly basal, flat or with involute margins, ascendent and rigid, rounded at the base, the apex acute, densely papillose-pilose on both surfaces, the margins ciliate. Peduncles long exserted, up to 30 cm long, filiform, pale or tinged with purple. Inflorescences terminal, exserted, with 2 racemes, occasionally with a single raceme or with a third raceme present; main axis up to 3 cm long, flat, smooth, glabrous, occasionally absent; pulvini glabrous, with a squamiform bract; racemes alternate, ascendent and divergent, ending in a developed spikelet; rachis of the racemes flat, straight, (2–)3–7 cm long, 1–1.6 mm wide, glabrous, the midnerve pale to green, the wings hyaline, nerveless, pale to purple; pedicels short, glabrous; spikelets solitary, imbricate and arranged in 2 series. Spikelets long-ellipsoid, 4–5 mm long, 1–1.1 mm wide without the hairs, plano-convex to slightly biconvex, acute, smooth, pilose; upper glume and lower lemma densely pilose on the lower half with white hairs, otherwise glabrous, the margins with papillose hairs, up to 2.5 mm long, reduced toward the apex. Upper glume as long as the spikelet, acute at the apex, with or without a short tuft of hairs, membranous, 3-nerved, with one central and two submarginal nerves. Lower lemma glumiform, as long as the spikelet or slightly shorter, 3–5-nerved. Upper anthecium long-ellipsoid, 3.2–4 mm long, 0.9 mm wide, 0.7–1 mm shorter than the spikelet, plano-convex, membranous to chartaceous; upper lemma with small papillae regularly distributed, and a tuft of macrohairs at the apex; lodicules 2, ca. 0.3 mm long, conduplicate; stamens 3, anthers 2 mm long; stigma plumose. Caryopsis long obovoid, 2 mm long, 0.9 mm wide; hilum elliptic; embryo ⅓ as long as the caryopsis.

Distribution and habitat. Endemic to central Brazil, where it grows in the Federal District and in the state of Goiás, in cerrados between 900 and 1200 m.

Paspalum goyasense is a close species of *P. carinatum,* the latter with filiform leaves, inflorescences usually with a single raceme, rachis of the racemes 1.8–2.5(–3.5) mm wide, spikelets with long hairs rising from the lower third, conspicuously scabrous on the rest of the surface, and apex of the upper glume and lower lemma dorsiventrally compressed and flat.

Representative specimens. BRAZIL. **Distrito Federal:** Brasília, *Irwin et al. 10257* (MO, US); 10 km W of Taguatinga, ruta a Braslandia, *Irwin et al. 10654* (MO, UB, US); Chapada da Contagem, ca. 20 km N de Brasília, *Irwin et al. 9648* (MO, US); Brasília, *Irwin et al. 9658* (MO, US); Brasília, Lago Sul, *Zuloaga 3835* (SI). **Goiás:** without locality, *Glaziou 22441* (G, US, W), *Glaziou 22443* (G, US, W); Serra dos Pirineus, 14 km S de Corumbá de Goiás, 16°S, 49°W, *Irwin et al. 10737* (MO, US); ca. 5 km N of jct. rd. W to Pires do Rio by BR 050, *Kral et al. 75939* (MO).

12. Paspalum heterotrichon Trinius, Sp. Gram. 3: pl. 285. 1829–1830. TYPE: Brazil. Without locality, *G. H. von Langsdorff 1829* (holotype, LE!; isotype, K! photo, SI!, US-2855297!). Figures 15, 16.

Paspalum gracile Schltdl., Linnaea 26: 134. 1854, hom. illeg. TYPE: Venezuela. Silla de Caracas, *Wagener 397* (not seen).
Paspalum heterotrichon Trin. var. *paucispicatum* Hack., Notizbl. Bot. Gard. Berlin-Dahlem 1(8): 328. 1897. TYPE: Haiti. Monte Furcy, 1896, *Picarda 1525* (holotype, W not seen; isotype, US-2855298!).
Paspalum ceresioides Carrillo, Revista Fac. Ci. Univ. Nac. S. Antonio 2: 145. 1968. Syn. nov. TYPE: Peru. Cuzco: Prov. Convención Chavuares, 920 m, 14 Abr. 1966, *C. Vargas C. 17215* (holotype, CUZ not seen; isotype, US!).

Caespitose, short-rhizomatous perennial, cataphylls pilose; culms (27–)45–90 cm tall, 1–1.9 mm diam., branching at the upper nodes or unbranched; internodes 2–3 cm long on the lower third and 6–12 cm long on the upper portion of the culms, terete, hollow, glabrous; nodes glabrous or pilose, with hairs white, 1–1.5 mm long. Sheaths (3–)5–12 cm long, glabrous or with the upper margins pilose. Ligules 0.5 mm long, membranous, truncate; pseudoligule present, a ring of hairs 3–4 mm long. Blades linear to linear-lanceolate, (4–)5–15 cm long, 1.5–4 mm wide, the abaxial surface glabrous, the adaxial one glabrous to sparsely pilose, the margins scabrous, attenuate, the apex acute. Peduncles (6–)10–16 cm long, terete, pilose. Terminal inflorescences 6–12 cm long, 2–2.5 cm wide; main axis (1–)2–4 cm long, 0.5 mm diam., pilose; racemes (1 to 2)3 to 7, (2–)3.5–6.5 cm long, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 3.5–4 mm wide, acuminate, glabrous, green at the middle portion and ferruginous at the wings, wings nerveless; pedicels 0.4 mm long, hispid, laterally inserted in the spikelets; spikelets solitary, arranged in 2 series. Spikelets ellipsoid, 2.3–3 mm long, 1–1.2 mm wide, pilose, upper glume and lower lemma subequal, with an annular thickening at the base. Upper glume as long as the spikelet, hyaline, acuminate, 3-nerved, with basal hairs ½ the length of the spikelet and papillose-pilose hairs at the margins, up to 3 mm long. Lower lemma membranous, acuminate, 3-nerved, with long hairs at the upper margins, otherwise glabrous. Upper anthecium ellipsoid, 1.5–1.8 mm long, 0.5 mm wide, glabrous, papyraceous; upper lemma with a tuft of macrohairs at the apex, and bicellular microhairs and silica bodies all over the surface; upper palea with prickles and silica bodies on the upper portion; lodicules 2, 0.1 mm long, rounded at the apex; stamens 3, anthers 1.2 mm long; stigma plumose. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 18, fig. 2. 1929. Swallen, Ann. Missouri Bot. Gard. 30: 93, fig. 18. 1943. Rodríguez, Ernstia 8(2–3): 38. 1998.

Distribution and habitat. *Paspalum heterotrichon* grows in Mexico, Central America (Honduras and Panama), and the Caribbean (Haiti and the Dominican Republic); in South America it is found in Colombia, Venezuela, Peru, and central Brazil, usually in open fields on limestone or rocky soils, between 300 and 2550 m elevation.

Paspalum heterotrichon shares with *P. petrense*, *P. trachycoleon*, and *P. phyllorhachis* ellipsoid spikelets, thickened at the base, upper glume hyaline, and rachis of the racemes winged. *Paspalum petrense* differs by the long-acuminate spikelets and lower lemma with a similar pilosity pattern of the upper glume, i.e., with long hairs at the base of the surface and the margins. *Paspalum trachycoleon* is distinguished by the paired spikelets, while *P. phyllorhachis* has glabrous spikelets.

The specimen *Macedo 1121*, probably a poorly developed plant, presents smaller spikelets than typical, 1.7–2 mm long, and culms 25–30 cm tall.

Internodes are occasionally markedly branching, 3 cm long and thinner, up to 0.6 mm in diameter.

In P and US (2855297) there is a specimen, *Riedel s.n.*, that probably belongs to the type collection of *P. heterotrichon* (see Renvoize, 1978, for comments on *Langsdorff* and *Riedel* collections).

Representative specimens. BRAZIL. **Distrito Federal:** Reserva Ecológica do IBGE, *Oliveira 719* (SI). **Goiás:** without locality, *Glaziou 22576* (G, K, P, W). **Mato Grosso:** Cuiabá, *Malme 1562b* (US). **Minas Gerais:** Mun. Itubitaba, *Macedo 1121* (MO). **Without state:** without locality, *Riedel 966* (G, SI), *s.n.* (P, US-2855297). COLOMBIA. **Magdalena:** Santa Marta, *Smith 143* (BM, COL, G, MO, P). DOMINICAN REPUBLIC. **Azua:** San Juan, Loma La Vieja, Cordillera Central, *Ekman 13404* (US). **Santo Domingo:** Cordillera Central, Prov. de la Vega, Costanza, Bajo de La Angostura, *Ekman 14018*

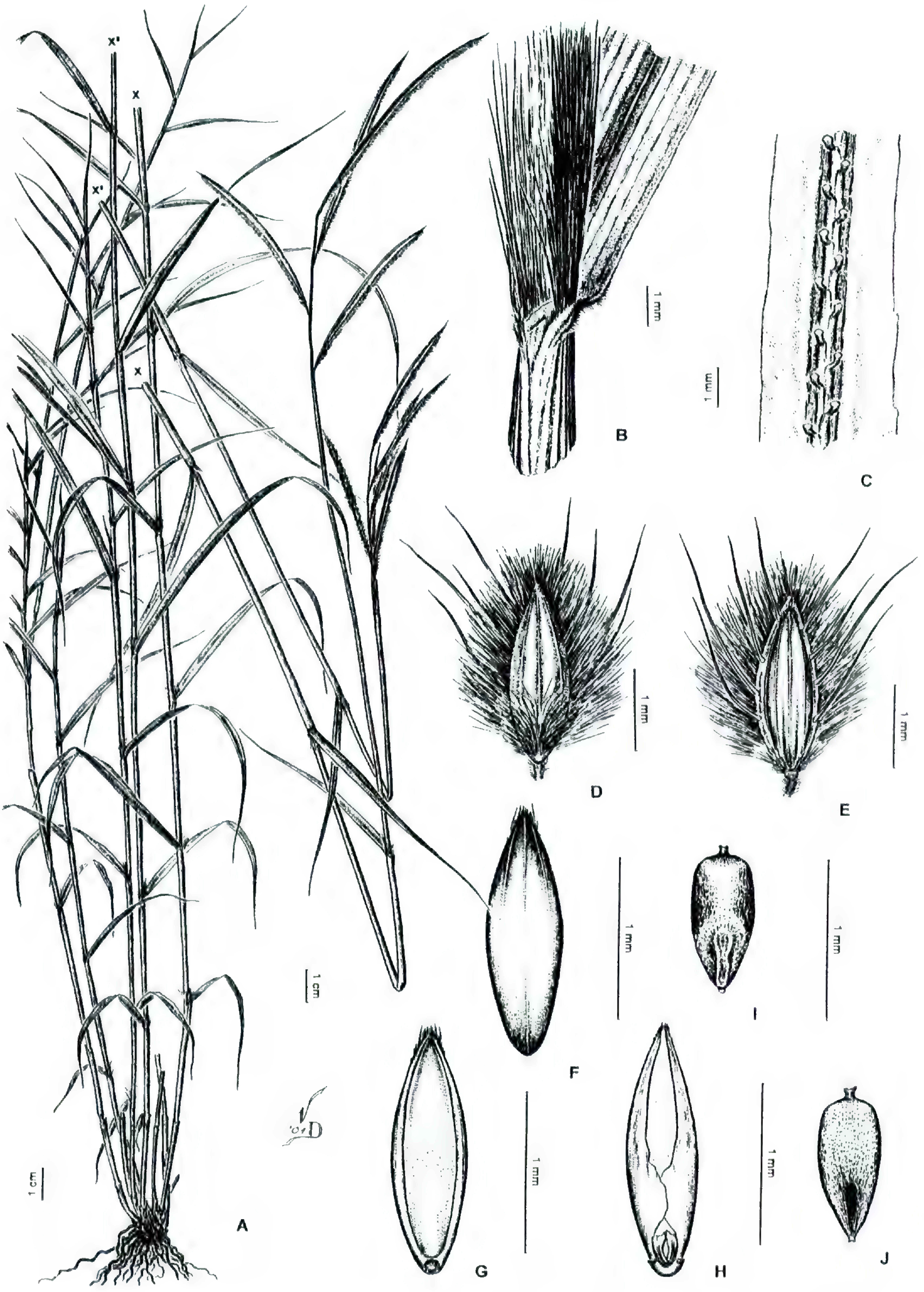

Figure 15. *Paspalum heterotrichon*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea with lodicules. —I. Caryopsis, scutellar view. —J. Caryopsis, hilum view. (A, B, D–J based on *Malme 1562b*, US; C based on *Tovar 4176*, US.)

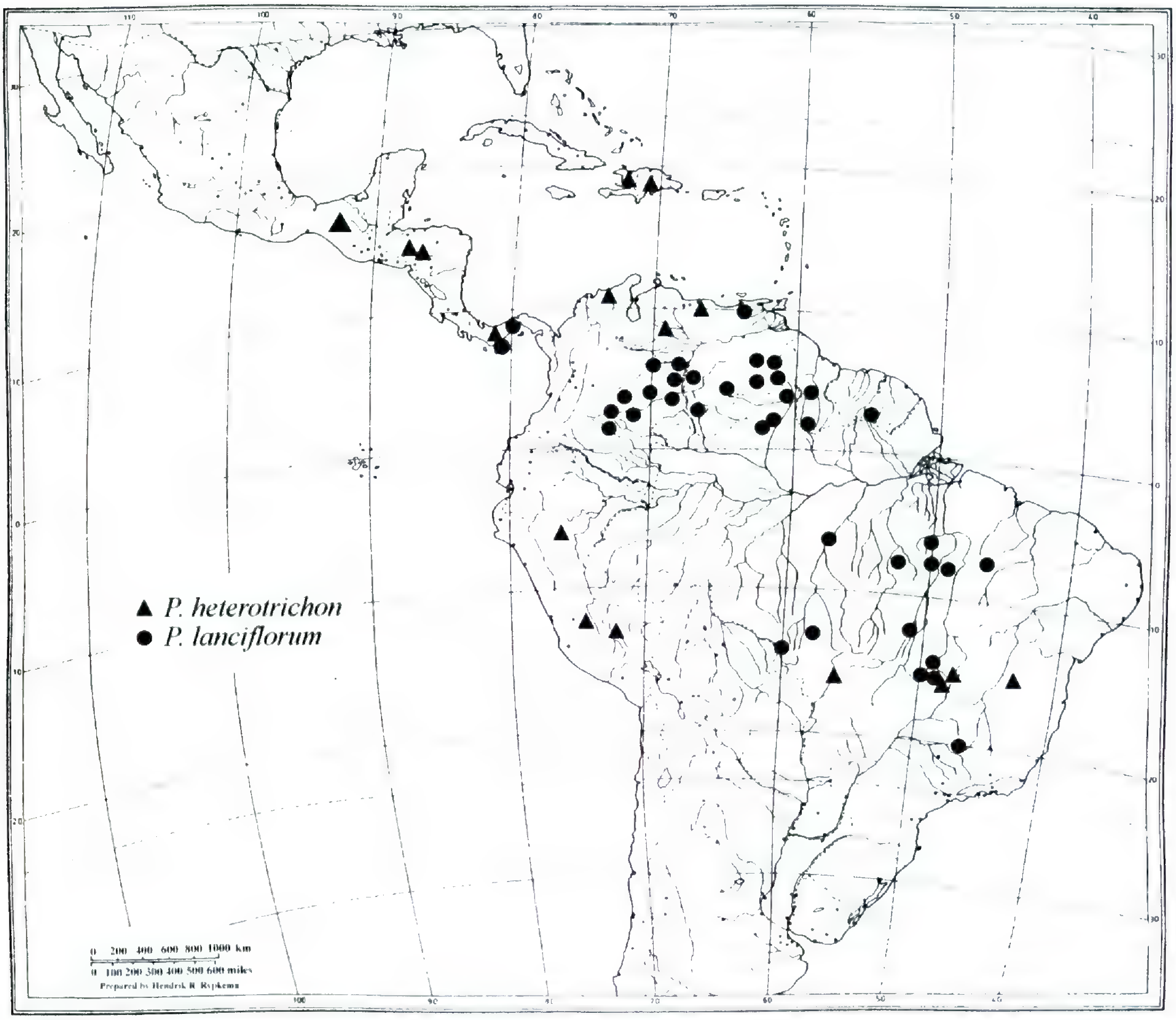

Figure 16. Distribution of *Paspalum heterotrichon* and *P. lanciflorum*.

(MO, US). HAITI. **du Nord:** vicinity of St. Michel de L'Atalaye, *Leonard 7793* (US). **l'Altibonite:** vicinity of Ennery, *Leonard 8953* (MO), *8957* (US); Frouin, eruptive hills above Chapelle Jubilée, *Ekman 2401* (G, US); Massif des Matheux, 26 Oct. 1924, *Ekman 2274* (US). HONDURAS. **Comayagua:** 4 km from San Isidro on the road to Pane, S side of rio Lima Gorge, *Moran 5505* (MO). **El Paraíso:** near km 2, road to Yuscarán, 5 Nov. 1951, *Swallen 11354* (MEXU, MO, US). **Francisco Morazán:** region of Las Mesas, *Swallen 10810* (MO, US), *11401* (US). MEXICO. **Chiapas:** El Pozo to Oxchuc, *Hernández Xolocotzi X-623* (US); Mun. Villa Corzo, above Colonia Vicente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54596* (MEXU, US). PANAMA. **Chiriquí:** near El Boquete, *Hitchcock 8297* (SI, US). PERU. **Amazonas:** Luya Province, Camporedondo, Fundo Cedro, 2450–2550 m, 24 Mayo 1989, *Días et al. 3493* (MO). **Huancavelica:** Huancavelica, Distrito de Huachocolpa, entre Marcavalle y Quintabamba, *Tovar 4176* (US). VENEZUELA. **Aragua:** 12 km S of Alto de Choroní along road to Maracay, *Davidse 3082* (K, MO); prope Colonia Tovar, *Fendler 1698* (G, K). **Lara:** Distr. Palavecino, Quebrada La Mata, towards the E side of the Parque Nac. Terepaima, *Burandt & Gantaume V0530* (MO).

13. Paspalum humboldtianum Flüggé, Gram. Monogr., Paspalum: 67. 1810, as "Paspalus humboldtianus." *Panicum humboldtianum* (Flüggé) Kuntze, Revis. Gen. Pl. 3(2): 361. 1898. TYPE: Ecuador: Puembo, *F. W. H. A. von Humboldt & A. J. A. Bonpland 3104* (holotype, B-W! photo, SI!; isotypes, BM!, P!, US-601340! photo, SI!). Figures 14, 17.

Paspalum distichophyllum Kunth, in H.B.K., Nov. Gen. Sp. 1: 86. 1816. TYPE: Colombia: Mesa de Cuello et Ibagué, Oct., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P!; isotypes, B!, US-2855276!).

Paspalum ciliatum Kunth, in H.B.K., Nov. Gen. Sp. 1: 87, pl. 24. 1816, hom. illeg. *Paspalum blepharophorum* Roem. & Schult., Syst. Veg. 2: 292. 1817. TYPE: Colombia: Ibagué y Valle de Caravajal, Monte Quindiu, Oct., *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, P!; isotypes, B!, US-2855275!).

Panicum obtectum J. Presl, Reliq. Haenk. 1: 301. 1830. *Tricholaena obtecta* (J. Presl) E. Fourn. ex Hemsl.,

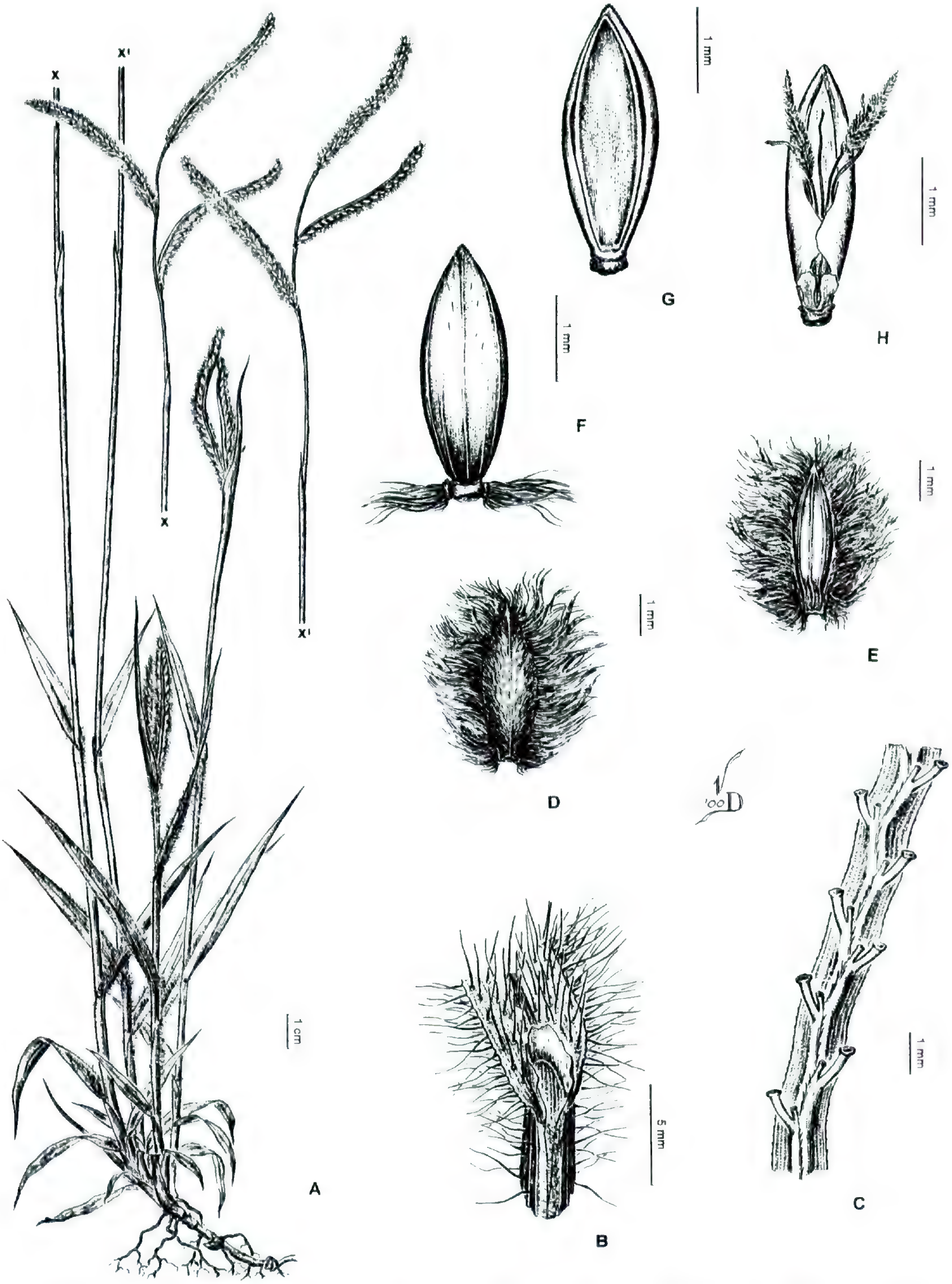

Figure 17. *Paspalum humboldtianum*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and gynoecium. (Based on *Zuloaga et al. 5887*, SI.)

Biol. Centr.-Amer., Bot. 3: 493. 1885, comb. illeg. *Tricholaena obtecta* (J. Presl) E. Fourn., Mexic. Pl. 2: 35. 1886. TYPE: Mexico. Without locality, *T. P. X. Haenke s.n.* (holotype, PR not seen; isotypes, US-2942536!, W).

Paspalum stuckertii Hack., in Stuck., Anales Mus. Nac. Buenos Aires 11: 63. 1904. *Paspalum humboldtianum* Flüggé var. *stuckertii* (Hack.) Hack., Allg. Bot. Z. Syst. 12: 97. 1906. TYPE: Argentina. Córdoba: Dpto. Punilla, Sierra Chica de Córdoba, en la punta de la Quebrada del Salto, del Ayo. Ochoa, 1000 m, 3 Apr. 1903, *T. J. V. Stuckert 13023* (holotype, W!; isotypes, BAA!, CORD!, G!, MO, US-80012! photo, SI!, US-557978!).

Paspalum soboliferum Chase, Contr. U.S. Natl. Herb. 24: 443. 1927. Syn. nov. TYPE: Ecuador. Loja: between Loja and San Lucas, 2100 m, 6 Sep. 1923, *A. S. Hitchcock 21495* (holotype, US-1164798! photo, SI!; isotype, S not seen).

Paspalum humboldtianum Flüggé var. *elegantissima* Beetle, Phytologia 52: 15. 1982. Syn. nov. TYPE: Mexico. Jalisco: 9 km from Los Volcanos, San José de Las Andrade, 29 Sep. 1980, *A. A. Beetle M-5962* (holotype, not located).

Short rhizomatous perennial, with leafy rhizomes; culms (30–)50–100 cm tall, 0.2–0.3 cm diam., erect or decumbent, lignified at the base, branching at the lower and middle nodes or unbranched; lower internodes 0.5–1 cm long, the upper ones 4–15 cm long, terete, hollow, glabrous or shortly pilose at the distal portion; nodes glabrous to pilose. Sheaths 4–11 cm long, longer than the internodes, overlapping, densely to sparsely papillose-pilose, with caducous tuberculate hairs at the upper portion, the margins ciliate. Ligules 1.2–2.5 mm long, membranous, brown, glabrous; pseudoligule absent; collar glabrous or pilose. Blades lanceolate, 5–21 cm long, 0.5–1.8 cm wide, flat, herbaceous, glabrous to sparsely pilose or hirsute, with long, tuberculate, caducous hairs, green to glaucous, shortly pseudopetiolate, the apex subulate. Peduncles exserted, up to 30 cm long, terete, glabrous. Terminal inflorescences exserted, 8–12 cm long, 3–5 cm wide; main axis 2–7 cm long, flat, with longitudinal nerves on the wings, scaberulous; racemes 2 to 6, ascendent, alternate and distant, slightly divergent from the main axis, ending in a naked point, occasionally in a spikelet; pulvini with a long tuft of white, rigid hairs; rachis of the racemes (3–)5–9 cm long, 1.2–1.5 mm wide, flat, shortly winged, green to purple, glabrous, scaberulous on the margins; pedicels unequal, up to 1.2 mm long, scaberulous; spikelets paired, and imbricate in 4 series, occasionally the lower spikelet aborted. Spikelets long-ellipsoid, 3–4 mm long, 1.2–1.4 mm wide, acute, plano-convex, pale or tinged with purple, the margins with long hairs; upper glume and lower lemma as long as the spikelet. Upper glume 3-nerved, hyaline, with plicate, corky margins covered with rigid, radiate and tuberculate hairs, 2–3.2 mm long, the rest of the surface sparsely pilose. Lower lemma 3-nerved, membranous, glabrous, scaberulous at the upper portion, depressed at the base. Upper anthecium ellipsoid, 2.6–3.2 mm long, 1–1.2 mm wide, membranous, pale, shiny, 0.4–0.6 mm shorter than the upper glume and the lower lemma; upper lemma 5-nerved, finely papillose with silica bodies, bicellular microhairs and prickles at the apex; upper palea papillose, with bicellular microhairs at the distal portion; lodicules 2, 0.6 mm long, truncate, conduplicate; stamens 3, anthers 1.6 mm long. Caryopsis not seen.

Common name. "Canutillo" (Venezuela).

Chromosome number. n = 10 (Hunziker et al., 1998); n = 20 (Saura, 1948); 2*n* = 40 (Tateoka, 1962).

Distribution and habitat. Found from Mexico and Central America to Bolivia and central and northwestern Argentina. It grows on mountain slopes, on loose, rocky to sandy soils; it is also common at margins of highways and in forest edges or modified areas, between 400 and 2900 m elevation.

Paspalum humboldtianum is related to *P. polyphyllum* and *P. buchtienii* by the upper glume with corky margins and covered with radiate hairs, the rachis usually ending in a spikelet. *Paspalum polyphyllum* differs by the narrow (0.1–0.6 cm wide), not pseudopetiolate, linear to linear-lanceolate blades, rachis pilose and with anastomosed veins, spikelets with the upper glume with unequal marginal hairs, and lower lemma pilose on the distal margins and the upper portion of the surface. Differences with *P. buchtienii* were summarized in the treatment of the latter species.

Paspalum humboldtianum usually has spikelets tinged with purple and anthers purple or dark brown; however, pale spikelets and anthers were observed in several specimens, such as *Zuloaga et al. 5885*.

The type material of *P. humboldtianum* var. *elegantissima* was not located; it should be mentioned that no herbarium was cited by Beetle (1980) when describing the species. However, the diagnosis allowed us to conclude that this variety is a synonym of *P. humboldtianum*.

When describing *P. soboliferum* based on a single collection from Ecuador, Chase (1927) distinguished the species from *P. humboldtianum* mainly by the shorter, more slender, and ascending racemes, spikelets 2.8–2.9 mm long, with short hairs toward the margins. Therefore, we considered the

type collection a poorly developed plant and placed *P. soboliferum* as a synonym of *P. humboldtianum*.

Spikelets with proliferous bracts were observed in several specimens from Mexico, such as *Müller 2036*, *Arséne 2813*, and *Schaffner 136*.

Representative specimens. ARGENTINA. **Catamarca:** Dpto. Andalgalá, Las Payvas, *Joergensen 1765* (LIL, MO, SI, US). **Córdoba:** Ascochinga, *Burkart 10211* (SI); Dpto. Punilla, Sierra Chica, *Stuckert 14159* (CORD, G, MO, SI). **Jujuy:** Río Perico, *Burkart & Troncoso 11014* (SI); Dpto. Tumbaya: Volcán, *Zuloaga et al. 5885* (SI). **La Rioja:** Velazco, *Soriano 986* (SI). **Salta:** Dpto. Capital, San Luis, *Filipovich 398* (LIL); Dpto. Candelaria, Cuesta de Muquillo, *Schreiter 9251* (LIL, MO, US). **San Luis:** Dpto. Gral. Pedernera, San José del Morro, Ea. La Morena, *Boelcke & Moore 16646* (SI). **Tucumán:** Tafí del Valle, *Burkart 5335* (SI); Dpto. Burruyacú, camino a Cerro Medina, *Villa Carenzo et al. 1818* (LIL). BOLIVIA. **Chuquisaca:** Sucre by the exit to Tarabuco, *Wood 7852* (US). **Cochabamba:** Morochata, *Cárdenas 3410* (LIL); W of Cochabamba, *Hitchcock 22830* (US). **La Paz:** viciniis Sorata, *Mandon 1254* (BM, G, P, US, W). **Santa Cruz:** 10 km E of Samaipa, *Renvoize & Cope 4038* (MO); Buena Vista, *Steinbach 6618* (BM, G, US). **Sucre:** Sucre, *Cárdenas 515* (US). **Tarija:** Camargo, *Fiebrig 3082* (G, LIL, SI, W). COLOMBIA. **Antioquia:** San Jerónimo, *Archer 629* (MA, US). **Boyacá:** without locality, *Saravia 4006* (COL). **Cauca:** Chisquío, Finca Los Derrumbos, *Asplund 10498* (G, US). **Cundinamarca:** La Esperanza, *Cuatrecasas 3001* (MA). **Huila:** 6 km SE of Altamira along road to Florencia, *Davidse et al. 5597* (COL, MO). **Norte de Santander:** vicinity of Pamplona, *Killip & Smith 19770* (US). **Providencia:** Pico-casabaja, *Idrobo 11636* (COL). **Santander:** Zapatoca, *Fassett 25502* (COL, US). **Without departament:** without locality, *Mutis 5537* (US). **Tolima:** Valle de San Juan, Cerro del Real Mina del Sapo, *Echeverry 1251* (COL). **Valle:** near Sevilla, *Barclay & Juajibioy 5703* (MO, US); Cordillera Occidental, E slope, Cali, Loma Los Cristales, *Cuatrecasas et al. 25702* (COL, US). COSTA RICA. **Cartago:** San Juan Norte, *Pohl et al. 11434* (US). **Guanacaste:** 2 km E of Liberia, *Pohl et al. 11327* (US). ECUADOR. **Azuay:** vicinity of Cuenca, along Río Milchichi, about 5 km N of Cuenca, *Camp E-2743* (G, US). **Chimborazo:** Chunchi-Alausi, *Acosta Solís 21454* (US). **Loja:** halfway between Loja and Catamayo, *Grignon 84257* (MO). **Oro:** between Portovelo and El Tambo, *Hitchcock 21306* (US). **Pichincha:** Tumbaco, *Asplund 6531* (G, P, US). **Tunguragua:** Ambato, *Hitchcock 21710* (US); Baños, *Asplund 7593* (G, P, US). EL SALVADOR. **Ahuachapán:** P.N. El Imposible, *Sermeño s.n.* (MO). **San Salvador:** San Salvador, *Calderón 1152* (US). GUATEMALA. **Alta Verapaz:** 5 mi. S of Cobán along Hwy. CA 14, *Thomas s.n.* (MO). **Santa Rosa:** Cerro Redondo, *Heyde & Luz 6271* (G). **Sololá:** Volcán San Pedro, *Steyermark 477177* (US). HONDURAS. **Francisco Morazán:** vicinity of El Zamorano, *Swallen 10776* (US). **Olancho:** Mun. La Unión, 5 mi. E of La Unión along road to Olanchito, *Davidse et al. 35448* (MO). MEXICO. **Chiapas:** 22 km NE of Motozintla on hwy. to Amatenango, *Stevens & Martínez 25701* (SI). **Colima:** Alzada, *Hitchcock 7055* (US). **Guanajuato:** ca. 8 km W of San Felipe on Cerro del Fraile, *Sohns 427* (US). **Guerrero:** Montes de Oca, Vallecitos, *Hinton 11400* (US). **Jalisco:** Mun. Tlajomulco de Zuñiga, Cerro Viejo region, 35–40 km due SSW of Guadalajara, *Machuca Nuñez 4640* (MO). **Michoacán:** Mun. Apatzingan, *Leavenworth & Leavenworth 1649* (US). **Morelos:** Cuernavaca, *Hitchcock 6837* (US). **Nayarit:** La Yesca, 23 km al SE de Puente de Camotlán, *Tenorio & Flores 16710* (MO). **Oaxaca:** Dist. Yautepec, Mun. Santa María Ecatepec, desviación a San Matías y Santa María Zapotitlán, *Flores Flanco et al. 3643* (MO). **San Luis Potosí:** 3 mi. SW of San Luis Potosí, *Reeder et al. 3313* (US). **Sonora:** Tepopa, Sierra Saguaribo, *Gentry et al. 19307* (US). **Tamaulipas:** Mun. Villa de Casas, central part of the Sierra de Tamaulipas, *Martínez & Luyando F-1953B* (US). **Veracruz:** Zacuapán, *Purpus 2002* (US). **Zacatecas:** Mun. Valparaiso, 1 km al N de San Francisco, *Rzedowski 17636* (US). NICARAGUA. **Nueva Segovia:** Santa María de los Pinos, 5 km NE de Dipilto, *Stevens & Montiel 24761* (MO). PANAMA. **Chiriquí:** Alto Boquete, *Partch 69-91* (MO); roadside near El Hato del Volcán, *Stockwell & Aiello 893* (MO, SI). PERU. **Amazonas:** Prov. Chachapoyas, 5 km W of Chachapoyas on road to Caclic, *Hutchison & Wright 4495* (G, MO, P, US). **Apurimac:** Challhuanaca, Aymaraes, *Núñez 7175* (MO). **Ayacucho:** Chumbes, *Balls 6923* (BM, US). **Cajamarca:** Prov. Chota, Yamaluc, a 11 km sobre la carretera Cochabamba–Huambos, *Sánchez Vega 2341* (SI). **Cuzco:** Prov. Convención, Amaybamba, *Marin 851* (US). **Huancavelica:** entre Izcuchaca y Acoria, *Tovar 1005* (US). **Lambayeque:** Prov. Chiclayo, Cerro Reque, *Llatas Quiroz 2322* (MO). **Lima:** entre Lunahuaná y Cañete, *Ferreyra 5373* (US). VENEZUELA. **Aragua:** Distr. Ricaurte, ca. 10–12 km SW of Colonia Tovar along the Colonia Tovar–La Victoria Hwy., *Davidse & Miller 28159* (MO). **Distrito Federal:** 5.5 km down road to Carayaca, *Davidse & Tillett 4073* (MO). **Lara:** Distr. Jiménez, 4–5 km S of Sanare, 9°42'N, 69°38'W, *Davidse & González 21370* (MO). **Mérida:** Sebastopol, *Chase 12294* (US). **Miranda:** Los Teques, *Burkart 16984* (SI). **Táchira:** Mun. Andrés Bello, Loma Blanca, Aldea Salomón, *Tamayo 2281* (US).

14. **Paspalum imbricatum** Filgueiras, Bradea 3: 153, fig. 2. 1981. TYPE: Brazil. Mato Grosso: Mun. Sidrolândia, Rod. BR-163, orla de brejo, 27 Oct. 1970, *G. Hatschbach 25281* (holotype, US-2705820! photo, SI!). Figure 25.

Caespitose perennial; culms 1–1.5 m tall, 0.3–0.5 cm diam., herbaceous to rigid, erect, unbranched; internodes 15–30 cm long, slightly compressed, hollow, glabrous, pale or tinged with purple; nodes brown, glabrous. Sheaths 15–25 cm long, densely hirsute, with papillose-pilose hairs at the distal portion, glabrous at the base, the margins membranous, shiny on both surfaces. Ligules membranous, 1–1.5(–2) mm long, brown, glabrous; pseudoligule a ring of hairs up to 1.3 mm long. Blades linear-lanceolate, 35–60 cm long, 0.6–1 cm wide, acute, pungent, mostly basal, flat, rigid, ascendent, the basal ones long pseudopetiolate, densely hirsute, with tuberculate hairs, on both surfaces. Peduncles up to 40 cm long, terete, glabrous, pale or purple. Terminal inflorescences exserted, 10–15 cm long, 8 cm wide; main axis 1.5–5.5 cm long, flat; racemes (2)5 to 7(11), (5–)10–14(–16) cm long, ascendent, slightly divergent from the main

axis, alternate, ending in a naked point; pulvini shortly pilose; rachis of the racemes 2.4–2.8(–3) mm wide, flat, the margins membranous to hyaline, nerveless, glabrous, green, shortly winged, wings purple; pedicels short; spikelets solitary, densely imbricate in 2 series. Spikelets broadly ovoid, 5–5.5 mm long, 2.8–3 mm wide, plano-convex, glabrous, pale, upper glume and lower lemma subequal, or the lower lemma slightly longer, cordate, the apex acute to almost rounded, the margins winged. Upper glume papyraceous, corrugate in the lower half, 5-nerved with 3 central nerves reaching the apex. Lower lemma glumiform, 5-nerved, corrugate in the lower half. Upper anthecium long-ellipsoid, 3.8–4 mm long, 1.2 mm wide, plano-convex, membranous, pale, pilose toward the apex, finely papillose; upper lemma with small papillae evenly distributed all over the surface, with macrohairs and bicellular microhairs at the apex, hispidulous toward the margins and in the lower portion; upper palea hispidulous toward the apex; lodicules 2, ca. 0.4 mm long, conduplicate, hyaline; stamens 3, anthers 2–2.5 mm long; stigmas 2, plumose, lateral. Caryopsis not seen.

Distribution and habitat. Endemic to Brazil, where it is found in cerrados in the Distrito Federal and the states of Mato Grosso and Goiás, between 950 and 1250 m elevation.

Paspalum imbricatum is a member of section *Pectinata*, sharing cordate upper glume and lower lemma, the margins winged; it is easily distinguished by the glabrous spikelets.

15. Paspalum lanciflorum Trinius, Sp. Gram. 3: pl. 286. 1829–1830. TYPE: Brazil. Mato Grosso: Cuiabá, 1829, *G. H. von Langsdorff s.n.* (holotype, LE!; isotype, US-80075!). Figure 16.

Paspalum contractum Pilg., Bot. Jahrb. Syst. 25: 709. 1898. TYPE: Colombia. Meta: Los Llanos de San Martín, Ago. 1868, *M. A. Stübel 190a* (holotype, B!; isotype, US-2942134!).

Paspalum echinotrichum Mez, Bot. Jahrb. Syst. 56, Beibl. 125: 9. 1921. TYPE: Brazil. Roraima: Rio Branco, Surumú, Sep. 1909, *E. H. G. Ule 8033* (lectotype, designated by Judziewicz (1990: 485), B!; isolectotypes, K!, US-2854675! photo, US).

Paspalum piligerum Swallen, Fieldiana, Bot. 28: 24, fig. 2. 1951. TYPE: Venezuela. Bolívar: Gran Sabana, between Kun and Uaduara–Paru, in valley of Rio Kukenan, S of Mount Roraima, 1065–1220 m, 1 Oct. 1944, *J. A. Steyermark 59090* (holotype, US-1911660!; isotype, F!).

Paspalum aureolatum Swallen, Fieldiana, Bot. 28: 22, fig. 1. 1951. TYPE: Venezuela. Territorio Federal Amazonas: summit of Cerro Duida, 1025–1200 m, 2 Sep. 1944, *J. A. Steyermark 58234* (holotype, US-1911652! photo, SI!).

Caespitose, shortly rhizomatous perennial; culms 45–120 cm tall, erect, unbranched; internodes 9–14 cm long, glabrous, brown; nodes glabrous to pilose, brown, compressed. Sheaths 9–17 cm long, densely hirsute on the distal portion, otherwise sparsely pilose or glabrescent, the adaxial surface shiny, brown. Ligules membranous, 1.5–3.2 mm long, glabrous, brown; pseudoligule a ring of hairs up to 0.8 cm long. Blades linear-lanceolate, 7–35 cm long, (0.3–)0.5–1(–1.5) cm wide, flat or with involute margins, densely papillose-pilose, with tuberculate hairs up to 7 mm long, the midnerve conspicuous on the adaxial surface. Peduncles long-exserted, up to 40 cm long, terete, glabrous. Terminal inflorescences subdigitate, yellow, occasionally with a papyraceous bract, up to 4 mm long, at the base; main axis absent or up to 1.5 cm long, glabrous, flat; pulvini pilose; racemes (1)3 to 6(11), ascendent, 5–15 cm long, subconjugate and ending in a naked point; rachis of the racemes (4–)5–7 mm wide, winged, green at the center, the midnerve white, with purple, membranous and glabrous margins; pedicels short, glabrous, flat; spikelets solitary, imbricate in 2 series. Spikelets long-ovoid, (4.8–)5.6–7.2 mm long, 1.2–2.5 mm wide, plano-convex, acuminate, pale, pilose. Upper glume as long as the spikelet, membranous, rounded and densely pilose at the base, the basal margins pilose, with hairs up to 2 mm long, otherwise glabrous, 3-nerved. Lower lemma slightly shorter than the upper glume, lanceolate, 3-nerved, densely pilose at the basal margins, the median portion with conspicuous, tuberculate hairs 2.5–3 mm long. Upper anthecium ovoid, 3.2–4.7 mm long, 0.9–2 mm wide, membranous, pale, stipitate, the stipe 0.3 mm long; upper lemma finely papillose, with bicellular microhairs and silica bodies at the apex, otherwise glabrous; lodicules 2, ca. 0.4 mm long, conduplicate; stamens 3, anthers 1.6 mm long; stigma lateral. Caryopsis not seen.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 26, fig. 7. 1929 (under *P. contractum*). Judziewicz, Fl. Guianas: 469, fig. 83, E. 1990.

Common name. "Pama" (Venezuela).

Distribution and habitat. Panama, Colombia, Guyana, Surinam, Venezuela, Brazil (Roraima, Pará, Maranhão, Mato Grosso, Minas Gerais, Goiás, and Distrito Federal), and Bolivia; it grows in savannas subjected to fire, on limestone, sandy, or rocky soils, between sea level and 1200 m.

Paspalum lanciflorum belongs to section *Pectinata*; within this section it is related to *P. cachim-*

boense, which differs by the annual habit, with branched, geniculate culms, rachis of the racemes 2–3 mm wide, spikelets 4–4.3 mm long, and upper anthecium 2.2–2.5 mm long. Also, *P. lanciflorum* is distinguished from *P. pectinatum* and *P. cordatum* by the glume densely pilose on the lower portion, not cordate, and upper anthecium stipitate, ⅓–½ the length of the spikelet.

This species is quite variable in its overall morphology. The specimens *Wurdack & Guppy 27*, *Tate 157*, and *Hahn et al. 5592b* are approximately 40–50 cm tall, with all blades basal. On the other hand, *Kuhlmann 1674*, *Glaziou 20084*, *22544*, and *Zuloaga et al. 4413* are more robust specimens, ca. 120 cm tall, with blades evenly distributed along the culms. It is noteworthy to mention the presence of densely papillose-pilose specimens, e.g., *Zuloaga et al. 4413*, *Tamayo s.n.*, *Egler & Raimundo 1262*, and others, as sparsely pilose, such as *Williams 13088* and *Maguire et al. 32038*.

Three to six racemes per inflorescence are frequent in this species; nevertheless, one to three racemes are found in *Swallen 4029*, *Williams 13088*, *Wurdack & Guppy 27*, *Gifford G-101*, *Oliveira & da Silva 700*, *Tamayo 3198*, *Ramirez 961*, and *Heringer et al. 4615*; the specimen *Echeverry et al. 2312* has 11 racemes per inflorescence.

Spikelets are small, 4.8–5 mm long, 1.7–2 mm wide in *Davidse et al. 22647* and *Blydenstein 1468*.

Chase (ined.) distinguished *P. contractum* from *P. lanciflorum* by the number of racemes (1 to 3 vs. 3 to 6) and the relative length of the lower lemma (as long as the spikelet vs. shorter than the spikelet). Our analysis of herbarium material did not allow us to distinguish between both taxa.

According to Judziewicz (1990), the specimen *Pohl 1454* (seen in B and W) is a syntype of the species; nevertheless, we examined at LE a specimen collected by *von Langsdorff* (see type material), and there are no elements that suggest Trinius had cited two syntypes when describing the species.

Representative specimens. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parque Nacional Noel Kempff Mercado, Campamento Las Gamas, *Killeen et al. 4929* (MO). BRAZIL. **Distrito Federal:** Brasília, Bacia do Rio S. Bartolomeu, *Heringer et al. 4615* (US); Serra de Arruda, *Glaziou 22544* (K, P, US); Serra Dourada, *Pohl 1454* (G). **Goiás:** Mun. Couto Magalhaes, 16 km W of Piqizeiro along GO-70, *Plowman et al. 19132* (US). **Maranhão:** Balsas, Morro antes do Rio Tem, *Oliveira & da Silva 700* (SI); Carolina to San Antonio de Balsas, *Swallen 4029* (US). **Mato Grosso:** ca. 270 km N de Xavantina, *Gifford G-101* (US); entre Barão de Capanema e Utiarity, *Kuhlmann 1674* (US). **Minas Gerais:** Ribeirão Taquarucu, *Glaziou 20084* (BM, K, P, US). **Pará:** Tapajós, Rio Cururú, *Egler & Raimundo 1262* (US). **Roraima:** Aldeia Tucham Paulo, para a base do Roraima, *Rondon s.n.* (US-2454780); Mt. Roraima, Paulo, *Tate 157* (US). COLOMBIA. Cravo Norte Arauca, al S del Río Meta, *Blydenstein 1468* (US). **Meta:** 13 km O de La Macarena, vía a Conejos, *Callejas & Marulanda 6886* (SI); carretera de Bella Vista a Piñalito, *Echeverry & Jaramillo 2312* (COL). **Vichada:** Mun. Puerto Carreño, Base Terecay, *Amat & Castillo 3* (COL). GUYANA. Potaro-Siparumi Region, Kato, *Hahn et al. 5592b* (US); Annai Hillside, *Goodland 923* (US). PANAMA. **Herrera:** ca. 7 mi. SW of Las Minas, *D'Arcy & Antonio 13527* (MO). SURINAM. Sipaliwini savana area on Brazilian frontier, *Oldenburger et al. 5* (US). VENEZUELA. **Amazonas:** Canaima, R. Carrao, *García Barriga 21426* (COL); Santa Bárbara savanna, junction of Ríos Ventuari and Orinoco, *Maguire et al. 32038* (US); alrededor del bajo Río Cataniapo, Pto. Ayacucho, *Williams 13088* (US). **Anzoátegui:** Dist. Bolívar, S of El Zamuro, Fila El Purgatorio, *Davidse & González 19314* (MO). **Bolívar:** El Pauji, *Liesner 19350* (SI); pié de la Roca to Guayaraca, *Davidse & Huber 22647* (MO); Gran Sabana, Vía Kavanayen, El Jardín, *Ramírez 961* (MO); Hato Santa Teresa, *Tamayo 3198* (MO); Hato La Vergareña, *Wurdack & Guppy 27* (US); 5 km al S de San Ignacio de Yuruaní, Gran Sabana, *Zuloaga et al. 4413* (K, SI, US).

16. Paspalum longiaristatum Davidse & Filgueiras, Novon 3: 129, fig. 1. 1993. TYPE: Brazil. Goiás: Mun. Niquelândia, Macedo, 14°18′S, 48°23′W, 13 Apr. 1992. *T. S. Filgueiras 2277* (holotype, IBGE!; isotypes, B not seen, BM!, FLAS not seen, ICN!, ISC not seen, K!, MEXU-62.8764!, MO!, NY not seen, P not seen, SI!, SP not seen, R not seen, RB not seen, UB not seen, UFG not seen, US not seen). Figure 23.

Caespitose annual; floriferous culms 15–36 cm tall, 0.8–1 mm diam., branching at the lower nodes; internodes terete, hollow, glabrous; nodes dark, pilose. Sheaths 3–7 cm long, papillose-pilose, the margins smooth. Ligules membranous-ciliate, the membranous portion 0.5–0.8 mm long, cilia 0.2–0.8 mm long. Blades linear, 3.5–8.2 cm long, 1–2 mm wide, attenuate at the base, papillose-pilose on both surfaces, more densely so toward the base. Peduncles terete, 0.5 mm diam., glabrous or with papillose-pilose hairs. Terminal inflorescences exserted, 5–8 cm long; main axis 1–2.5 cm long, papillose-pilose, ending in a naked point; racemes 1 to 2(4), 2–7 cm long, alternate, arcuate, ascendent and divergent; pulvini pilose; rachis of the racemes membranous, 4–6 mm wide, winged, hyaline, and ciliate at the margins, the adaxial surface with papillose-pilose hairs, the abaxial surface glabrous; pedicels 0.1–0.2 mm long, hispid; spikelets solitary, imbricate in 2 series. Spikelets ellipsoid, 1.8–2.2 mm long, 0.5–0.6 mm wide, pilose, brown or tinged with purple, shiny. Upper glume hyaline, 3-nerved with one central and two marginal nerves, pilose at the base, the hairs reaching ½ the length

of the spikelet, the margins pilose with ascendent hairs, awned, awn 6–12.2 mm long, scabrous. Lower lemma glumiform, slightly shorter than the upper glume, membranous, 3-nerved, awned, awn 0.3–2 mm long, scabrous. Upper anthecium ellipsoid, 1.5–1.8 mm long, 0.7–0.8 mm wide, membranous, shiny; upper lemma 5-nerved, with prickles, bicellular microhairs and silica bodies at the upper portion; upper palea 2-nerved; lodicules absent; stamens 3, anthers 1.4–1.8 mm long, purple at maturity; stigma plumose. Caryopsis 1–1.2 mm long, 0.4–0.5 mm wide; hilum punctiform, basal, embryo more than half the length of the caryopsis.

Distribution and habitat. Endemic to central Brazil, in the state of Goiás, where it is found in cerrados, in serpentine, rocky soils at 1000 m.

Paspalum longiaristatum differs from *P. biaristatum* by the perennial habit, spikelets 3.8–4.5 mm long, awn of the upper glume 4–7.1 mm long, and awn of the lower lemma 3.8–4.5 mm long of the latter taxon.

Representative specimens. BRAZIL. **Goiás:** Macedo, ca. 15 km N of Niquelândia, *Brooks et al. 144* (MO); Macedo, a 18 km de Niquelândia, *Filgueiras 2342* (K, MO, SI, US), *Filgueiras 2780* (MO, US), *Oliveira et al. 638* (US); km 23 ao 3 da estrada de terra a direita da mina de niquel, *Fonseça et al. 227* (MO, SI); Mun. Alto Paraiso, Vale da Lua, 14°10′S, 98°47′S, *Filgueiras & Oliveira 3292* (US).

17. Paspalum malmeanum Ekman, Ark. Bot. 10: 12, tab. 4, fig. 3. 1911. TYPE: Brazil. Mato Grosso: Santa Ana da Chapada, 31 May 1903, *G. O. A. Malme s.n.* (holotype, S not seen; isotype, US-80089!). Figure 23.

Caespitose, shortly rhizomatous perennial; culms 60–90 cm tall, few-noded; internodes 6–10 cm long, purple, terete, hollow, striate; nodes glabrous. Sheaths usually longer than the internodes, slightly compressed, glabrous, pale or tinged with purple, shiny, the margins ciliate or glabrous. Ligules membranous, 0.2 mm long, brown, glabrous; pseudoligule a ring of hairs up to 1.2 mm long. Blades linear, 10–45 cm long, 0.1 cm wide, involute, papillose on the adaxial surface, glabrous and smooth on the abaxial surface, the margins papillose-pilose toward the base with hairs up to 6 mm long, otherwise glabrous, the apex subulate. Peduncles exserted, terete, up to 35 cm long, glabrous. Terminal inflorescences exserted; main axis absent; pulvini with a tuft of short hairs and occasionally with 2 small bracts on the basal pulvini; racemes 2, conjugate, 7–14 cm long, occasionally with a single raceme present; rachis of the racemes 1.2–2 mm wide, ending in a naked point, purple or with the margins red-tinged, glabrous, the wings flat; pedicels subterete, glabrous to short pilose at the apex; spikelets solitary, densely imbricate in 2 series. Spikelets ellipsoid, 1.6–2 mm long, 0.8–1.2 mm wide, villous, early deciduous, upper glume and lower lemma subequal. Upper glume membranous, 3-nerved, the margins rigid, densely pilose at the basal portion with short and appressed, tuberculate hairs, the margins ciliate, silky with hairs up to 1.5 mm long, the rest of the surface glabrescent. Lower lemma glumiform, 3-nerved, pilose at the margins and ⅔ of the surface. Upper anthecium obovoid, 1.5 mm long, 0.8–1 mm wide, plano-convex, membranous, pale, shiny, rounded at the apex; upper lemma smooth; lodicules 2, 0.1 mm long, conduplicate; stamens 3, anthers 1 mm long. Caryopsis ellipsoid, 1 mm long; hilum punctiform, embryo less than ½ the length of the caryopsis.

Chromosome number. $2n = 20$ (Killeen, 1990).

Distribution and habitat. *Paspalum malmeanum* grows in Bolivia and Mato Grosso, Brazil, where it is usually found in flooded savannas on sandy soils between 0 and 500 m elevation.

Paspalum malmeanum is related to *P. eucomum*, which differs by the spikelets 2.5–3 mm long. Other features of its distribution and habitat are pointed out in the treatment of *P. eucomum*.

Representative specimens. BOLIVIA. **Santa Cruz:** Velasco, Parque Nacional Noel Kempff M., campamento Los Fierros, *Gutiérrez et al. 655* (MO); Ñuflo de Chávez, 3 km SW of Concepción on road around reservoir, *Killeen 2024* (G, LPB, MO, SI, US); Ñuflo de Chávez, Est. Las Madres, *Killeen 2076* (MO, SI, US); Ñuflo de Chávez, Estancia Santa María, *Killeen 2478* (MO, SI, US). BRAZIL. **Mato Grosso:** NW of São Lourenço, E of Rio Ibo, *Chase 11962* (MO, US); Juruena, *Kuhlmann 1667* (US); caminho da Guia Linha Telegrafica, *Kuhlmann 1668* (US).

18. Paspalum niquelandiae Filgueiras, Novon 5: 30, fig. 1. 1995. TYPE: Brazil. Goiás: Mun. Niquelãndia, ca. 14°18′S, 48°23′W, ca. 2 km este da localidad de Macedo, 19 May 1993, *T. S. Filgueiras & F. C. de A. Oliveira 2461* (holotype, IBGE!; isotypes, F not seen, G not seen, ICN not seen, K!, MEXU not seen, MG not seen, MO!, R not seen, SI!, SP not seen, US not seen). Figure 23.

Rhizomatous perennial; culms 120–185 cm tall, 0.4–0.6 cm diam., unbranched; internodes 5–8, glabrous, hollow; nodes glabrous, dark. Sheaths glabrous or pilose toward the base and papillose-hispid toward the distal portion, keeled, the margins ciliate or glabrous. Ligules 0.2–0.3 mm long, membranous; pseudoligule a ring of hairs 5–8 mm long. Leaf blades lanceolate, 20–45 cm long, 0.8–

2.2 cm wide, acuminate, flat, glabrous to papillose-hispid, the margins scabrous or ciliate. Peduncles exserted, 12–22 cm long, glabrous. Terminal inflorescences 14–18 cm long, 6–9 cm wide; main axis 9–15 cm long, glabrous, terete or wavy; racemes 8 to 30, 2.5–8.5 cm long, alternate, ascendent, ending in a naked point, occasionally in a spikelet; pulvini pilose, with 2–2.5 mm long hairs; rachis of the racemes 1–1.5 mm wide, foliaceous, flexuous toward the apex, glabrous or scabrous, midnerve manifest and wings with thin, longitudinal nerves; pedicels 0.1–0.3 mm long, scabrous; spikelets paired, arranged in 4 series. Spikelets ellipsoid to ovoid, 2.3–3.3 mm long, 1–1.4 mm wide, pilose, plano-convex. Upper glume membranous, 3-nerved, the margins corky, with radiate, tuberculate hairs 0.3–1 mm long, the rest of the surface glabrous or shortly hispid. Lower lemma flat, membranous, 3-nerved, glabrous, as long as the upper glume, depressed at the base. Upper anthecium ovoid, 2.2–2.7 mm long, 1–1.1 mm wide, membranous to chartaceous, glabrous; upper lemma 5-nerved, with simple papillae regularly distributed all over the surface and sparse bicellular microhairs; lodicules 2, 0.1–0.2 mm long; stamens 3, anthers 1.2–2 mm long; stigmas plumose. Caryopsis not seen.

Distribution and habitat. Endemic to the state of Goiás, Brazil, where it grows on outcrops of serpentine, rocky soils, near edges of gallery forests.

Paspalum niquelandiae is related to *P. burmanii* and *P. humboldtianum.* Differences with *P. burmanii* were summarized in the treatment of that species. In *Paspalum humboldtianum* plants are (30–)50–100 cm tall, with branched or unbranched culms, two to six racemes per inflorescence are present, and spikelets are long ellipsoid, with radiate hairs, 2–3.2 mm long, at the margins of the upper glume.

19. Paspalum pectinatum Nees ex Trinius, Sp. Gram. 1: pl. 117. 1828. *Paspalum pectinatum* Nees, Fl. Bras. Enum. Pl. 2: 34. 1829, hom. illeg. *Anastrophus pectinatus* (Nees ex Trin.) Schltdl. ex B. D. Jacks., Index Kew. 1: 118. 1893. TYPE: Brazil. Without locality, *F. Sellow s.n.* (holotype, LE not seen; isotypes, B!, G!, K! photo, SI!, LE not seen, US-2942525!, W!). Figures 18, 19.

Caespitose, shortly rhizomatous perennial; floriferous culms 35–100 cm tall, erect, few-noded; internodes 2 to 4, 7–14 cm long, 0.2 cm diam., hollow, slightly compressed, striate, glabrous; nodes glabrous, brown. Sheaths usually longer than the internodes, the basal ones shiny, red-tinged to brown, glabrous; upper sheaths green, keeled, villous to hirsute all over the surface or only toward the upper portion, the margins membranous. Ligules membranous, 0.3–0.5 mm long, brown, glabrous; pseudoligule a tuft of white hairs 3–4 mm long. Leaf blades linear, 10–30 cm long, 0.2–0.8 cm wide, mostly basal, flat or with involute margins, densely pilose on both surfaces, the base attenuate, the apex acute. Peduncles long-exserted, up to 30 cm long, finely striate, glabrous. Terminal inflorescences with 2(3 to 5) conjugated, ascendent racemes, 2–8 cm long; main axis absent or up to 1 cm long; pulvini shortly pilose; rachis of the racemes shortly winged, 2–2.5 mm wide, glabrous, membranous, green, with light-brown to purple, crenate, glabrous or pilose, margins, the midnerve manifest, ending in a naked point; pedicels up to 0.6 mm long, flat, glabrous; spikelets solitary, densely imbricate and arranged in 2 series. Spikelets lanceolate, 5–8 mm long, 2–3.3 mm wide, dorsiventrally compressed, slightly plano-convex, cordate, the apex acute, pilose, pale or tinged with purple. Upper glume as long as the spikelet, 3–5-nerved, winged, papyraceous to hyaline, cordate, slightly convex, glabrous, the base cordate, corrugated at the middle portion. Lower lemma 4.5–7.2 mm long, 3-nerved, not winged, sparsely pilose, subcordate, the margins papillose-pilose with rigid, tuberculate hairs 1–2.5 mm long. Upper anthecium ellipsoid, 4–5 mm long, 1.4–1.6 mm wide, plano-convex, papyraceous, pale; upper lemma finely papillose, with bicellular microhairs, short macrohairs and isolated silica bodies at the distal portion and along the margins; palea smooth; lodicules 2, ca. 0.4 mm long, hyaline, conduplicate; stamens 3, anthers 2 mm long, ferruginous; styles 2, free, stigma plumose, lateral. Caryopsis not seen.

Common name. "Grama-das-pedras" (Brazil).

Chromosome number. n = 10 (Davidse & Pohl, 1978; Pohl, 1980); 2*n* = 40, 60 (Gould & Soderstrom, 1967).

Distribution and habitat. This species grows from southern Mexico, Mesoamerica, Colombia, Venezuela, Guyana, and Surinam to Bolivia, Paraguay, and central and southern Brazil, mainly in savannas on sandy soils with rocky outcrops. It is frequent in areas with periodical fires, occasional in margins of streams, between 180 and 1800 m elevation.

Paspalum pectinatum is a member of section *Pectinata* by its winged and cordate upper glume. This species is related to *P. cordatum*, a species distinguished by its robust plants, 100–130 cm tall,

Figure 18. *Paspalum pectinatum*.—A. Habit. —B. Detail of ligule. —C. Spikelet, ventral view. —D. Spikelet, dorsal view. —E. Upper anthecium, dorsal view with lateral stigmatic plumules. —F. Upper anthecium, ventral view with lateral stigmatic plumules. —G. Upper palea, lodicules, anthers, and gynoecium. (Based on *Filgueiras 2459*, SI.)

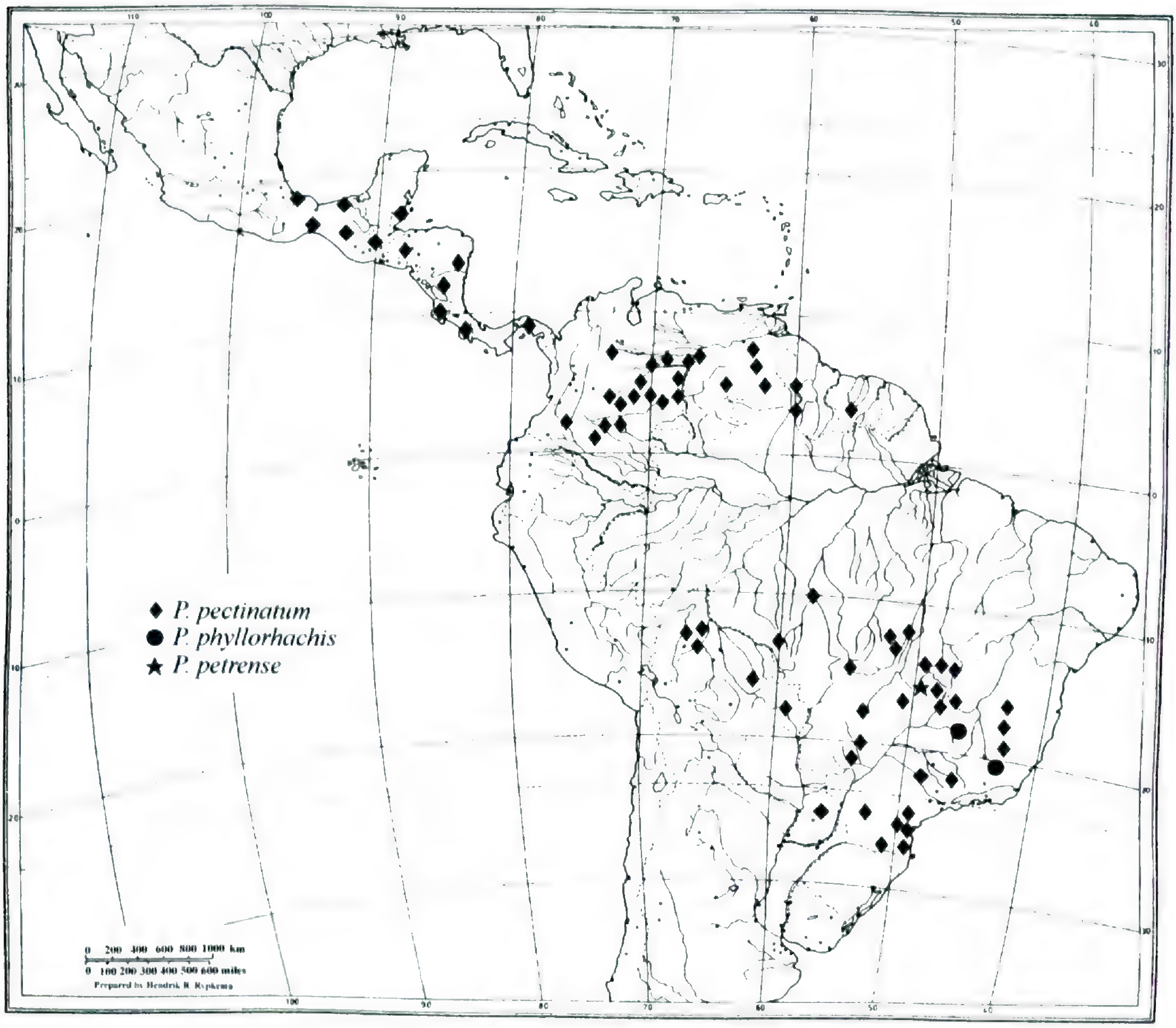

Figure 19. Distribution of *Paspalum pectinatum*, *P. petrense*, and *P. phyllorhachis*.

with 5 to 10 racemes per inflorescence, each raceme 12–16 cm long.

The basal portion of the plant is usually covered with remains of burnt sheaths, which probably act as a protection for the renewal buds.

The specimens *Fonseca et al. 153*, *Oliveira et al. 763*, and *Filgueiras 2459*, collected in Goiás, Niquelândia, Brazil, have 8 to 9 internodes with leaf blades arranged along the floriferous culms.

There is a papyraceous bract at the base of the inflorescence, as in *Rivera 3*, *Pinto & Sastre 1066*, *Rivera L-141*, *Davidse 5321*, and *Cuatrecasas 7649-A*.

Representative specimens. BELIZE. **Belize:** along Manatee (or Coastal) Hwy., 7.4 km S of Turnoff to Gales Point, *Nee & Atha 46904* (MO). BOLIVIA. **Beni:** Prov. Vaca Diez: Riberalta, 65 km hacia Santa Rosa, cerca del desvío a Cobija, *Beck 20552* (K). **La Paz:** Prov. Iturralde, Luisita, *Haase 630* (K, MO). **Santa Cruz:** Chiquitos, 4 km W of Santiago de Chiquitos, *Killeen 2782a* (MO, US). BRAZIL. **Distrito Federal:** Brasília, lago Sul, *Zuloaga 3839* (SI). **Goiás:** Mun. Niquelândia, Macedo, ca. 20 km de Niquelândia, *Filgueiras 2455* (MO); Campo de Pichoce, *Glaziou 22427* (BM, K, MO, P, US). **Mato Grosso:** Expedition Base Camp, *Argent 6766* (K, P, US); ca. 70 km N of Xavantina, *Irwin & Soderstrom 6758* (K, MO, SI). **Minas Gerais:** Serra do Espinhaço, ca. 10 km SW of Diamantina, *Anderson et al. 35213* (MO); Diamantina, Serra de San Antonio, *Chase 10350* (MO, US). **Paraná:** Ponta Grossa, *Araujo 104* (SI); Jaguariaiva, *Dusén 16057* (MO, P, SI). **Santa Catarina:** Campo Novo, Mafra, *Klein 3916* (US). **São Paulo:** Bôa Vista, 4–5 km SE da Estação Eng. Hermilo, *Machado de Campos 111* (US). **Without locality:** *Sellow 1232, 1239* (B). COLOMBIA. **Arauca:** N del río Tame, *Blydenstein 734* (COL). **Boyacá:** near Orocué, *Haught 2709* (COL). **Caquetá:** Mun. San Vicente del Caguán, Hato Caquetania, *Bentacur & Porras 1510* (MO). **Cauca:** Chisquito, *Asplund 10633* (US); Río Guaviare, San José del Guaviare, *Cuatrecasas 7649-A* (COL, US). **Cundinamarca:** savanna of San Martín, SE of Bogotá, *Shaw s.n.* (US). **Guaviare:** Mun. San José del Guaviare, Inspección de La Fuga, *Giraldo-Canas & López 2631* (MO). **Meta:** 20 km SE of Villavicencio, *Alston 7569* (BM, COL, US); Mun. Puerto Gaitán entre Carimagua y El Porvenir, *Rivera 3* (COL). **Santander:** La Laguna, carretera Lebrija–Pantano, *Rivera L-141* (COL). **Vichada:** Parque Nacional Natural Tuparro, *Barbosa & Zarucchi*

3032 (MO); ca. 45 km E of Cumaribo along dirt road between Las Gaviotas and Santa Rita, *Davidse & Llanos 5321* (COL). COSTA RICA. **Guanacaste:** Comelco, W of Bagaces, *Heithanus 163* (MO). **San José:** Cantón de Acosta, Fila Bustamante, *Morales 4395* (MEXU, MO). **Puntarenas:** Buenos Aires, *Pohl & Clark 13922* (MO). GUATEMALA. N of the San Pedro, *Semple 150* (US). GUYANA. Hillsides, Amai, *Graham 520* (K). HONDURAS. **Copán:** Hacienda Espíritu Santo, *Blake 7445* (US). MEXICO: **Chiapas:** Mun. Palenque, 2–4 km N of La Victoria and 7–9 km NWN of Palenque, *Davdise 20544* (MEXU, MO). **Oaxaca,** Mun. Sta. María Chimalapa, El Ocotal Grande, ca. 5 km al E de Sta. María, *Hernández 2283* (MO). **Tabasco:** km 64 rumbo Huimanguillo-Fco. Rueda al O de Huimanguillo, *Hill & Cowa 1548* (MEXU). **Veracruz:** a 11 km del entroque Las Choapas con la carretera Cardenas–Coatzacoalcos, *Orozco 182* (MEXU). NICARAGUA. **Chontales:** 15 km SE of Juigalpa, along Hwy. 7, *Pohl & Davidse 12361* (MO). **Zelaya:** near Cano Alamikamba, 26.5 km SE of El Empalme by road to Limbaika, *Kral 69245* (MO). PANAMA. **Chiriquí:** Cerro Vaca, eastern Chiriquí, *Pittier 4351* (US); Cerro Campana, *Lazor 3350* (MO). SURINAM. Sipaliwini savanna, *Rombouts 308* (US). PARAGUAY. **Canendiyú:** Mbaracayú Natural Reserve administered by Fundación Moisés Bertoni, 24°11′S, 55°16′W, *Zardini & Ramirez Benítez 51117* (MO). VENEZUELA. **Amazonas:** E of Caño Parucito and N of its tributary Caño Majagua, *Jangoux 10153* (MO). **Apure:** Distrito Pedro Camejo, 22 km W de Galeras de Cinaruco, *Davidse & González 15652* (MO). **Bolívar:** SW of La Vergareña, S of Ciudad Bolívar, *Alba 53–23* (US).

20. Paspalum petrense A. G. Burman, Kew Bull. 35: 297. 1980. TYPE: Brazil. Goiás: Serra de Pirineus, ca. 20 km E of Pirenópolis, 8 Apr. 1979, *T. S. Filgueiras & A. G. Burman 430* (holotype, K!; isotypes, IBGE!, SP not seen, RB-217458!). Figures 19, 20.

Caespitose perennial; culms erect, 70–90 cm tall, unbranched; internodes terete, hollow, glabrous or sparsely pilose toward the summit; nodes glabrous. Sheaths 7–10 cm long, papillose-pilose toward the apex, overlapping, keeled. Ligules ca. 1 mm long, membranous, truncate; pseudoligule absent. Blades linear to linear-lanceolate, 10–19 cm long, 3–6 mm wide, pubescent, the margins scabrous, attenuate at the base, the apex acute. Peduncles 17–30 cm long, pilose at the apical portion. Terminal inflorescences 8–15 cm long, 4–7 cm wide; main axis glabrous; pulvini pilose; racemes 3 to 5, 3–6 cm long, alternate, ending in a naked point; rachis of the racemes (6.5–)7–7.5 mm wide, foliaceous, glabrous, green to purple, with anastomosed veins on the wings, the margins slightly scabrous; pedicels 0.4–0.6 mm long, hispid, laterally inserted in the spikelets; spikelets paired, the basal one sometimes reduced or aborted, arranged in 2 to 4 series. Spikelets ellipsoid, 3–3.5 mm long, 1–1.1 mm wide, long-acuminate, pilose, pale, upper glume and lower lemma subequal, with an annular thickening at the base. Upper glume membranous to hyaline, 3-nerved, hairy on the lower half, the margins papillose-pilose. Lower lemma membranous to hyaline, acuminate, 3-nerved, pilose on the lower half with hairs shorter than those of the upper glume. Upper anthecium ellipsoid, 2.8–3 mm long, 0.6–0.8 mm wide, membranous, shiny, with a tuft of hairs at the apex, otherwise glabrous; upper lemma and upper palea with bicellular microhairs and papillae all over the surface and silica bodies at the apex; lodicules 2, 0.1 mm long; stamens 3; stigma plumose. Caryopsis not seen.

Distribution and habitat. Endemic to central Brazil, Goiás, where it is present in rocky soils on mountain slopes, at an elevation of 1200 m.

Paspalum petrense is related to *P. heterotrichon* (see observations under this species) and *P. trachycoleon. Paspalum petrense* differs from *P. trachycoleon* by its unbranched culms (vs. branching culms), rachis (6.5–7.5 mm vs. 4–6 mm wide), the upper glume long-acuminate (vs. acute to acuminate), and lower lemma long-acuminate, pilose, not sulcate, and with inconspicuous nerves (vs. acute, glabrous or with short, apical hairs, sulcate, and with conspicuous nerves).

21. Paspalum phyllorhachis Hackel, Oesterr. Bot. Z. 51: 240. 1901. TYPE: Brazil. Minas Gerais: without locality, 1872, *A. F. M. Glaziou 20078* (holotype, W!; isotypes, B!, K! photo, SI!, US-2855768! photo, SI!). Figures 19, 21.

Shortly rhizomatous perennial; culms 70–170 cm tall, 2–7 mm diam., erect or climbing, bambusiform, branching at the lower and middle nodes; internodes 5–8 cm long, glabrous, terete, hollow, lignified; nodes glabrous, brown. Sheaths 5–8 cm long, glabrous or pilose at the upper portion, keeled, the margins smooth, glabrous. Ligules membranous, 1.5–2 mm long, truncate to rounded at the apex, decurrent; pseudoligule absent. Leaf blades linear-lanceolate, 7–17 cm long, 0.4–1.3 cm wide, rounded, long-acuminate at the apex, with the abaxial surface glabrous to pilose and the adaxial surface densely pilose, margins smooth to scabrous. Peduncles exserted, glabrous or pilose toward the distal portion. Terminal inflorescences exserted, 10–13 cm long, 1.5–3 cm wide; main axis 4–9.5 cm long, 0.5 mm diam., glabrous or pilose; racemes 7 to 14, (2.5–)3.5–5 cm long, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 4–6 mm wide, foliaceous, with anastomosed nerves on the wings, glabrous, brown; pedicels 0.8 mm long, hispid, laterally inserted in the spikelets; spikelets paired, imbricate in 4 series. Spikelets

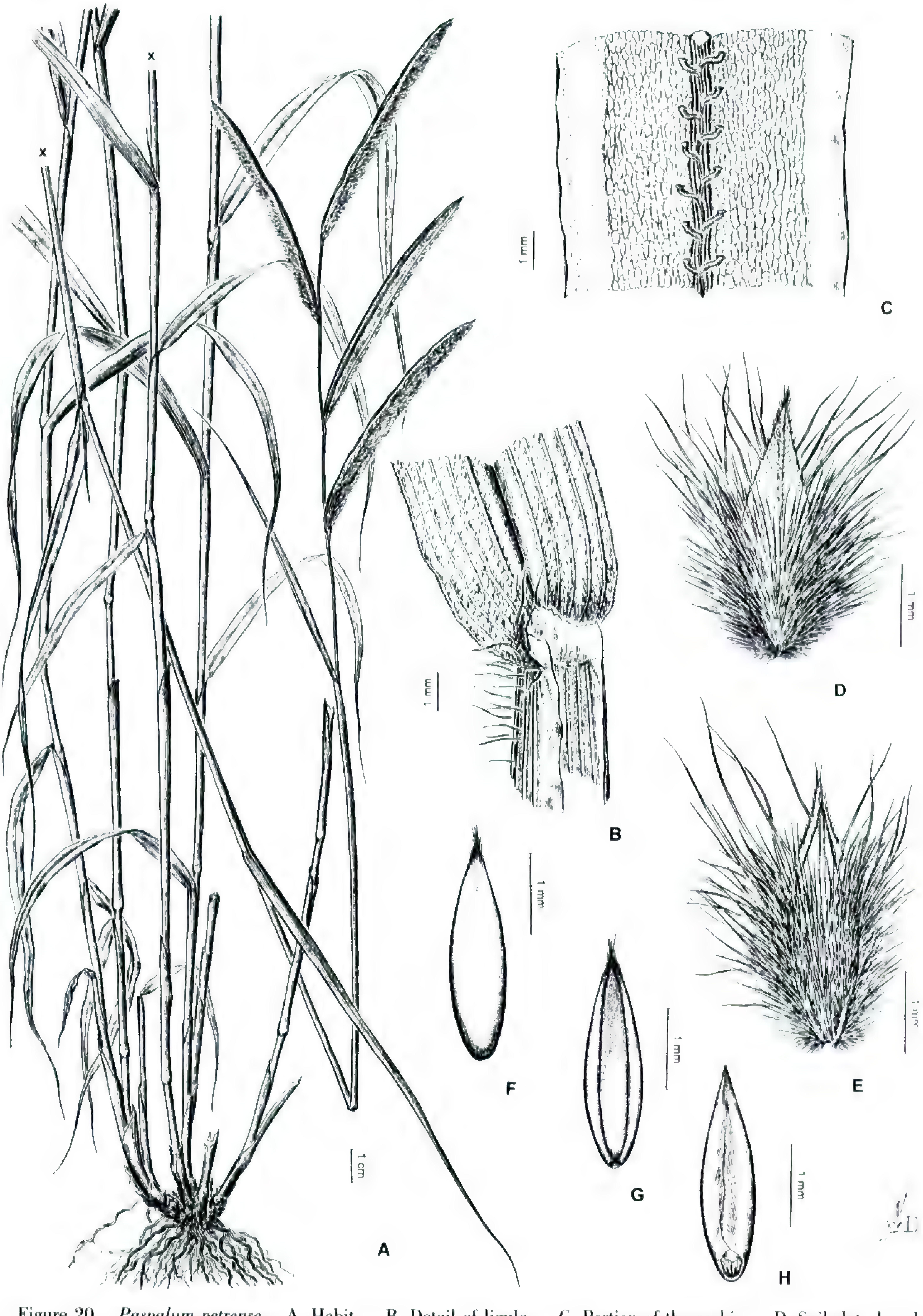

Figure 20. *Paspalum petrense*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea and lodicules. (Based on *Filgueiras & Burman 430*.)

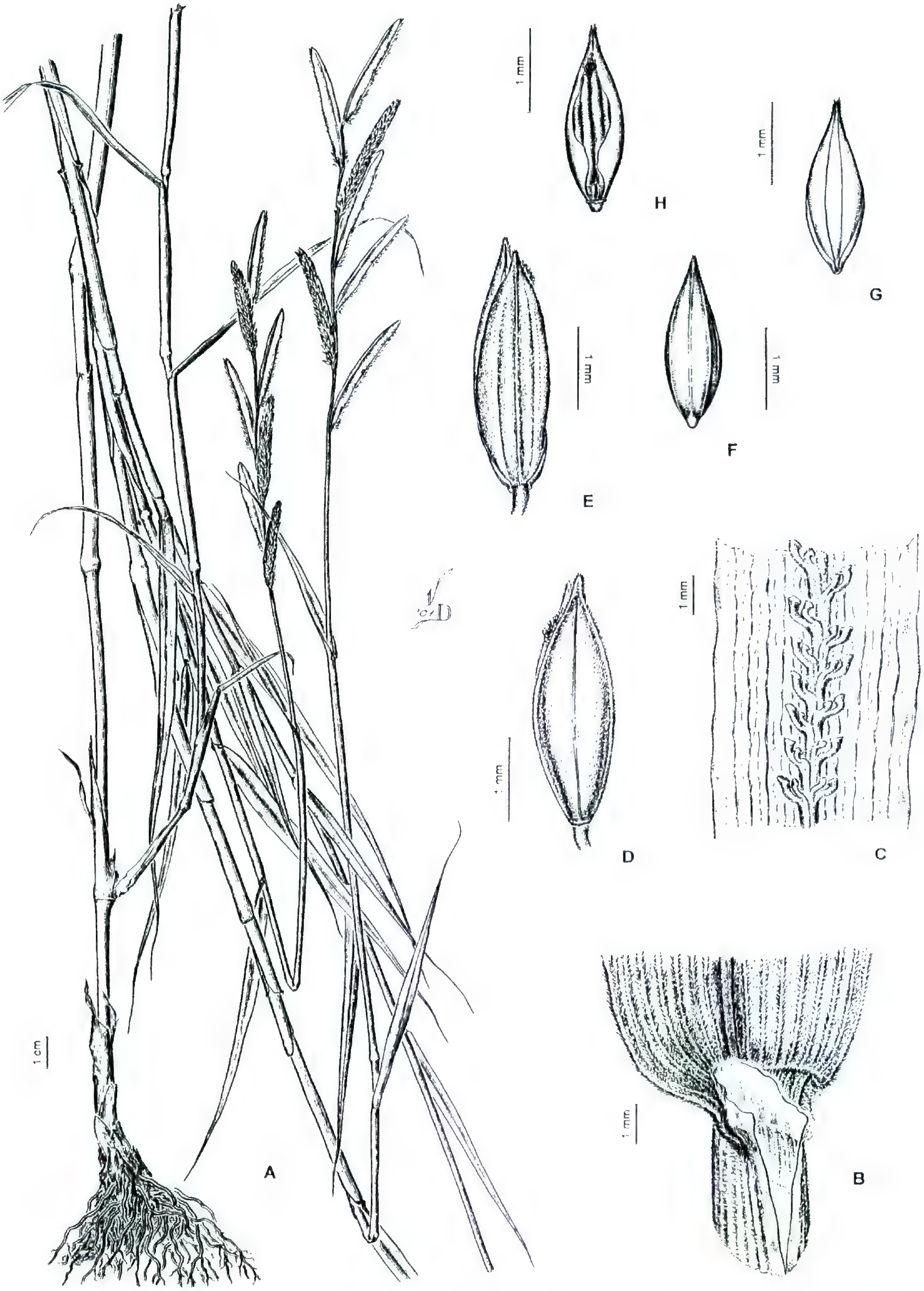

Figure 21. *Paspalum phyllorhachis*.—A. Habit. —B. Detail of ligule. —C. Portion of the rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Upper palea, lodicules, and anthers. (A based on *Chase 8975*, US; B–H based on *Glaziou 20070*, P.)

ellipsoid, 2.3–2.8 mm, 0.8–1 mm wide, glabrous, upper glume and lower lemma subequal, scabrous at the upper margins. Upper glume as long as the spikelet, acuminate, hyaline to membranous, 3-nerved. Lower lemma glumiform, acuminate, membranous, 3-nerved. Upper anthecium lanceolate, 2.1–2.7 mm long, 0.7–1 mm wide, membranous, scabrous at the apex, otherwise glabrous; upper lemma and palea with conspicuous, simple papillae and bicellular microhairs all over the surface, and prickles at the apical portion; stamens 3, anthers 1.5 mm long; stigma plumose. Caryopsis not seen.

Distribution and habitat. Endemic to Brazil, Minas Gerais, where it is found in open fields between 1200 and 1400 m elevation.

Paspalum phyllorhachis is related to *P. petrense* and *P. trachycoleon* by its paired spikelets. It differs from both species by these spikelets being glabrous.

Glabrous and pilose spikelets were occasionally observed in the specimen *Magalhães Gomes 908*, with sparse hairs toward the apical margins of the upper glume.

Representative specimens. BRAZIL. **Minas Gerais:** Serra do Curral, S of Belo Horizonte, *Chase 9325* (US), *8975* (US); Rios das Pedras a Matto Grande, *Glaziou 20070, 20076* (P); Belo Horizonte, *Magalhães Gomes 908* (US-1762607).

22. Paspalum polyphyllum Nees ex Trinius, Gram. Panic. 114. 1826. *Paspalum polyphyllum* Nees, Fl. Bras. Enum. Pl. 2: 41. 1829, hom. illeg. TYPE: Brazil. Chapada, "in campis siccis pr. Mariannam," 1824, *G. H. von Langsdorff s.n.* (holotype, LE!; isotypes, K! photo, SI!, US-2855764! photo, SI!). Figures 7, 22.

Paspalum blepharophorum Roem. & Schult. var. *tenue* Döll, in Mart., Fl. Bras. 2(2): 67. 1877. TYPE: Brazil. Without locality, *L. Riedel s.n.* (lectotype, designated here, W!; isolectotype, G!).

Paspalum macroblepharum Hack., Oesterr. Bot. Z. 51: 196. 1901. TYPE: Brazil. Rio de Janeiro: without locality, 1887, *J. Arechavaleta 41* (holotype, W!; isotype, US-2855810! photo, SI!).

Paspalum bicilium Mez, Repert. Spec. Nov. Regni Veg. 15: 27. 1917. TYPE: Brazil. Goiás: Fazenda do Siriaco, cascada do Rio Macaco, 12 July 1895, *A. F. M. Glaziou 22563* (lectotype, designated here, B!; isolectotypes, BR not seen, K!, P! photo, SI!, US-2942158!).

Caespitose perennial, with long, arcuate rhizomes, cataphylls coriaceous, villous; culms (10–)25–90 cm tall, 0.1–0.2 cm diam., rigid, branched or unbranched, erect, occasionally decumbent; internodes 1–10 cm long, terete, hollow, glabrous; nodes brown, glabrous or shortly pilose. Sheaths 1.5–8 cm long, usually longer than the internodes, glabrous to hirsute, with tuberculate hairs, the margins glabrous or shortly ciliate. Ligules 0.4–2.5 mm long, membranous, brown, glabrous; pseudoligule, when present, a tuft of rigid hairs 2.4–5 mm long; collar glabrous to shortly pilose. Leaf blades linear to linear-lanceolate, 4–13 cm long, 0.1–0.6 cm wide, flat, rigid, ascendent, glabrous to papillose-pilose on both surfaces, narrow or rounded at the base, the apex subulate, the margins short to long papillose-pilose. Peduncles exserted, up to 30 cm long, terete to filiform, glabrous to hirsute in the distal portion. Terminal and axillary inflorescences exserted; terminal inflorescences 4–12 cm long, 0.4–3(–4) cm wide; main axis absent or 1–4(–7) cm long, sulcate, glabrous to hirsute; pulvini shortly pilose, with white hairs up to 0.6 mm long; axillary inflorescences 4–7 cm long, 0.5–3 cm wide; racemes 1 to 4(8), ascendent, slightly divergent from the axis, straight, alternate, ending in a naked point, sometimes in a spikelet; rachis of the racemes 3–10 cm long, 1–1.2 mm wide, pilose or with adaxial surface glabrous, green or tinged with purple, with anastomosed veins, the margins scabrous and covered with long hairs; pedicels unequal, up to 1.7 mm long, triquetrous, hispid; spikelets paired, densely arranged in 4 series, sometimes lower spikelet aborted. Spikelets long-ellipsoid, 1.4–3.8 mm long, 0.6–1.2 mm wide, acute, pilose, the margins rigid, purple, covered with long, ciliate spreading hairs; upper glume and lower lemma as long as the spikelet, hyaline. Upper glume with corky margins covered with radiate, white hairs 2–7 mm long, alternating with shorter hairs 0.8–2 mm long, otherwise shortly pilose, 3-nerved. Lower lemma hyaline, the margins shortly pilose, hairs up to 0.5 mm long, the rest of the surface glabrous to sparsely pilose, convex and depressed toward the base, 3-nerved. Upper anthecium long-ellipsoid, 1.2–3.6 mm long, 0.6–0.8 mm wide, acute, membranous, pale, with bicellular microhairs and simple papillae all over the surface and macrohairs and silica bodies toward the apex of the upper lemma and palea, upper lemma 3-nerved; lodicules 2, ca. 0.2 mm long, conduplicate, hyaline; stamens 3, anthers 0.8–2 mm long. Caryopsis long-obovoid, 0.8–1.3 mm long, 0.4–0.6 mm wide; hilum linear, ⅓ the length of the caryopsis; embryo ⅓ to ½ the length of the caryopsis.

Common name. "Capim-lanoso" (Brazil).

Distribution and habitat. From Venezuela and Colombia to central and southern Brazil, Bolivia, Paraguay, northeastern Argentina, and Uruguay. This species grows in open fields and savannas, on

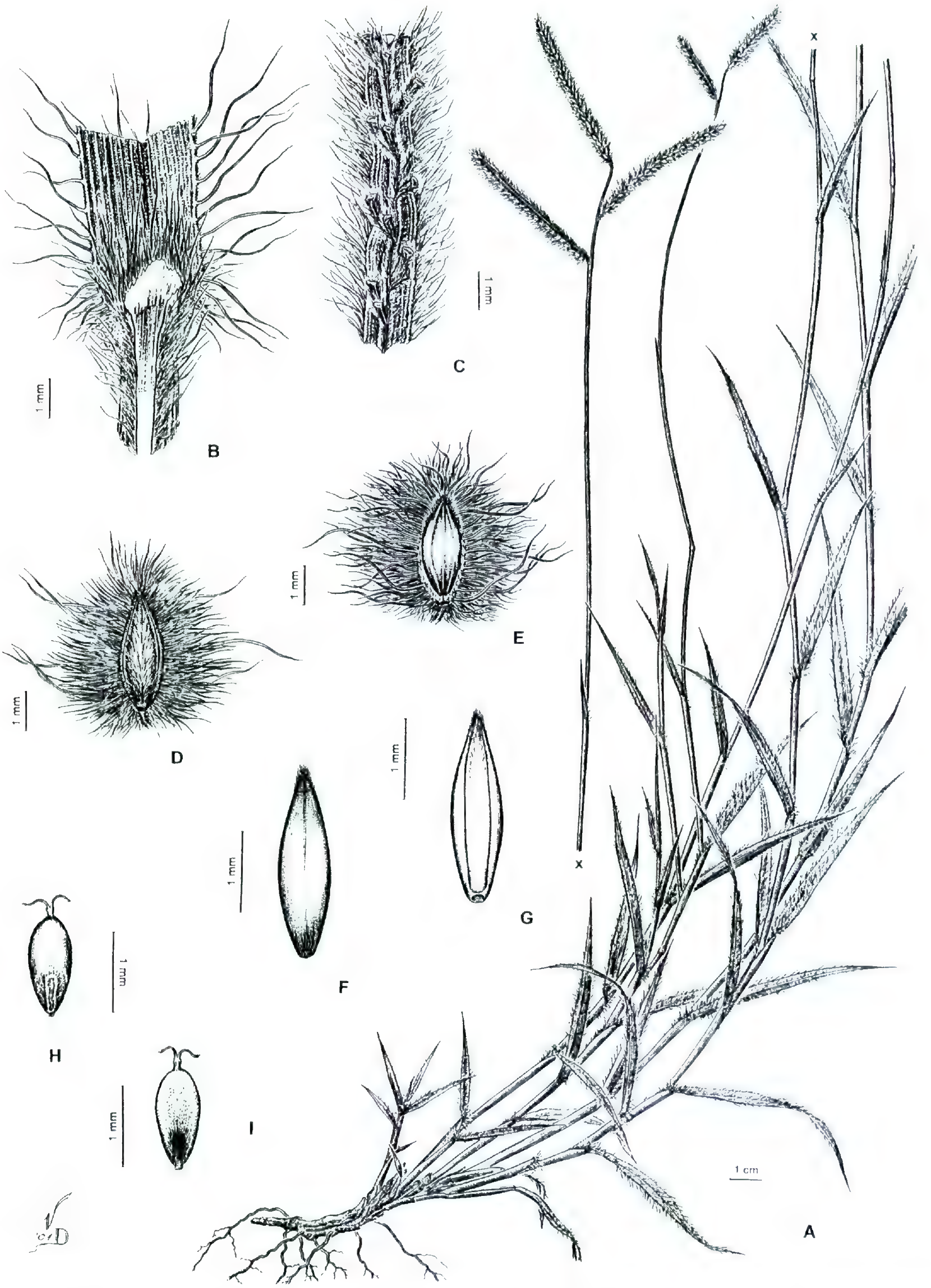

Figure 22. *Paspalum polyphyllum*.—A. Habit. —B. Detail of ligule. —C. Portion of rachis. —D. Spikelet, dorsal view. —E. Lemma, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (Based on *Smith & Klein 12106*, US.)

rocky, sandy soils, occasionally in swamps, between 0 and 2500 m.

Paspalum polyphyllum shows a high degree of plasticity in its vegetative characters, such as plant height, branching, blade pilosity, and size of inflorescences and spikelets. This species has two different growing patterns; one of them, with simple culms bearing larger inflorescences and spikelets of different size, from 2.6 to 3.6 mm long (e.g., *Swallen 8772, Smith & Klein 12106, Hassler 11561, Schulz 17275, Archer & Barreto 4995,* and *Fiebrig 6222*) or more than 4 mm, e.g., *Rojas 13933,* which also have inflorescences more than 19 cm long, racemes 11–13 cm long, and spikelets 4–4.2 mm long. The other phase is characterized by its culms profusely branching at the middle nodes, with smaller inflorescences and spikelets ca. 2 mm long (as in *Irwin et al. 16232a, 17256, Killeen 2795, Hunt & Ferreira Ramos 6012, Hunt 6246,* and *Chase 9148*). Also, both phases can be found in a single collection, e.g., *Swallen 9150,* where simple, erect culms up to 40 cm tall, with spikelets 3 mm long, are mixed with more delicate culms in which spikelets are 2 mm long. It is noteworthy to mention that the type material of *P. polyphyllum* belongs to the second phase of development.

When studying type material of *Paspalum bicilium* and *P. macroblepharum* it became evident that they belong to the branching phase of *P. polyphyllum,* with spikelets up to 2 mm long.

Doell (1877) cited, following the concept of Trinius (1828–1836, figs. 134, 144), under *P. blepharophorum* and *P. distichophyllum* what here is considered *P. polyphyllum,* including in *P. blepharophorum* specimens of the unbranching phase and in *P. distichophyllum* specimens of the branching one. Both species are here considered synonyms of *P. humboldtianum* (see synonymy under this species).

Doell (1877) cited three syntypes when describing *P. blepharophorum* var. *tenue,* of which *Riedel s.n.* was here selected as lectotype of the species; of the remaining syntypes, *Sellow s.n.* also belongs to *P. polyphyllum,* and *D'Orbigny 168,* from Chuquisaca, Bolivia, probably belongs to *P. humboldtianum.*

The number of racemes is higher, ranging from 4 to 12, in the specimen *Chase 9369.*

Mez (1917) cited two syntypes when describing *P. bicilium, Glaziou 22562* and *22563,* of which the latter has been selected as lectotype of the species.

According to Rosengurtt et al. (1970) this species is a low-yield forage grass.

Representative specimens. ARGENTINA. **Chaco:** Dpto. San Fernando, Fontana, *Meyer 2090* (LIL); Dpto. 1° de Mayo, Colonia Benítez, *Schulz 17275* (G, MO, SI). **Corrientes:** Dpto. Paso de Los Libres, Campo Militar Gral. Avalos, *Carnevali 3200* (CTES, LIL). **Misiones:** Dpto. San Ignacio, sobre Ruta Prov. 210 m, a 7 km Ayo. Horqueta, *Honfi 98* (LIL, MO); Puerto Nuevo, *Schwarz 2214* (B, LIL, US). BOLIVIA. **La Paz:** Puente Villa-Yungas, *Cárdenas 3606* (US). **Santa Cruz:** Prov. Chiquitos, S slope of the Serrania de Santiago, *Daly et al. 2171* (MO, SI); Chiquitos, Serrania de Santiago, *Killeen 2795* (MO); Buena Vista, *Steinbach 6808* (BM, G, K, MO, W, US). BRAZIL. **Bahia:** Mun. Palmeiras, Pai Inácio, BR-242, km 232, *Mori 13303* (K, MO); Dpto. Palmeiras, Morro do Pai Inacio, *Zuloaga & Morrone 6944* (IBGE, SI). **Distrito Federal:** a 32 km do CENARGEM, *Borges Dias Vieira 189* (MO); Parque Municipal do Gama, ca. 20 km S of Brasília, *Irwin & Soderstrom 5800* (MO, SI, US). **Goiás:** Serra do Caiapó, ca. 33 km S of Caiaponia on road to Jataí, *Irwin & Soderstrom 7069* (K, MO, SI); between Jataí and Caiaponia, 45 km from Caiaponia, *Hunt 6246* (K, US); Serra Azul, about 7 km W of the Barra do Garcas, *Hunt & Ramos 6012* (K, US). **Mato Grosso:** ca. 6 km S of Xavantina, *Argent et al. 6460* (P, US); Serra do Roncador, Rio Turvo, *Irwin et al. 16232a* (MO); summit, Serra Azul, *Irwin et al. 17256* (US). **Minas Gerais:** without locality, *Glaziou 20082* (P, US, W); Serra do Cipó, Chapeu de Sol, Santa Luzia, *Archer & Barreto 4995* (US); Serra do Cipó, 110 km NE of Belo Horizonte, *Chase 9148* (MO); Ouro Preto, Villa Rica, *Chase 9369* (MO, US). **Paraná:** 13 km NE of Atuba (which is just outside of Curitiba) along Hwy. 116, *Davidse et al. 10967* (MO); Ponta Grossa, Fazenda de Criaçao, *Swallen 8772* (US). **Rio de Janeiro:** Itatiaia, *Brade & Vianna 20377* (US); environs de Rio de Janeiro, *Glaziou 17940* (G, MO, W). **Rio Grande do Sul:** Montenegro, *Araujo 144* (US); Pelotas, *Swallen 9150* (US). **Santa Catarina:** Mun. Mafra, campo 10 km NW of Mafra on the road to Barracas (20 km), *Smith & Klein 12106* (US). **São Paulo:** Est. Biológica do Inst. Bot. Paranpiacaba, *Dedecca 302* (US). COLOMBIA. **Boyacá:** Villa de Leyva cerca de Sáchica, *Saravia 4186* (COL). **Santander:** Mesa Los Santos, *Robinson & Beltran 3189* (US). PARAGUAY. **Alto Paraná:** in regione fluminis Alto Paraná, *Fiebrig 6222* (BAA, BM, G, LIL, SI, US). **Amambay:** in campis arenosis Estrella, *Hassler 10209* (G, US). **Caaguazú:** Caaguazú, *Balansa 90a* (G, P). **Central:** in regione lacus Ypacaray, *Hassler 11501* (MO). **Cordillera:** Piribebuy, Colonia Pedro Caballero, *Rojas 13404* (LIL-561328). **Guairá:** Borja, *Montes s.n.* (LIL-561328). **Paraguarí:** Cerro Peron, prés de Paraguarí, *Balansa 90* (BM, G, P, US, W). URUGUAY. **Artigas:** Artigas, *Berro 2680* (BAA, W). **Cerro Largo:** Palleros, *Herter 1755* (G, MO, US). **Flores:** Río Yí y Ayo, Matanzas, *Montoro s.n.* (US-1723957). **Paysandú:** Río Uruguay y Chapicuy, *Rosengurtt B-3197* (LIL, US). **Rivera:** Tranqueras, *Castellanos 17922* (LIL). **Tacuarembó:** without locality, *Osten 6632* (SI, US). VENEZUELA. **Lara:** Distr. Morán, Carretera de Humocaro Bajo via Buenos Aires, *van der Werff & Rivero 7863* (MO). **Trujillo:** La Cristalina, *Tamayo 1867* (US).

23. Paspalum reticulinerve Renvoize, Kew Bull. 50: 339, fig. 1 A–G. 1995. TYPE: Bolivia. La Paz: Prov. Iturralde, Siete Cielos, Río Manupare, ca. 2.5 km al E, 12°27′S, 67°37′W, 180 m, 8 June 1987, *J. C. Solomon 17003* (holotype, LPB not seen; isotypes, K!, MO!). Figure 14.

Shortly rhizomatous perennial; floriferous culms (70–)90–120(–140) cm tall, 0.3 cm diam., erect, branched or unbranched; internodes finely striate, glabrous, hollow; nodes 5 to 7, compressed, brown, glabrous. Sheaths 15–24 cm long, usually longer than the internodes, keeled toward the upper portion, glabrous to hirsute, the inner surface red-tinged-brown, shiny, the margins membranous, glabrous. Ligules membranous, 1–2.5 mm long, brown, glabrous; pseudoligule absent or a tuft of hairs 5–7 mm long. Blades linear-lanceolate, 17–40 cm long, 0.3–0.8 cm wide, flat, glabrous to hirsute, the base attenuate and the apex acute, the margins involute, with long hairs toward the lower portion, otherwise scaberulous. Peduncles up to 40 cm long, terete, glabrous. Terminal inflorescences exserted, 5–15 cm long; main axis absent or up to 1 cm long, flat, glabrous; pulvini shortly pilose; racemes (1)2(3), 5–15 cm long, ending in a naked point; rachis of the racemes winged, 1–1.8 mm wide, green or tinged with purple, glabrous to sparsely pilose, the midnerve scabrous and margins scaberulous to papillose-pilose; pedicels unequal, flat, scaberulous; spikelets paired, densely imbricate in 4 series. Spikelets broadly ovoid, 4.8–6 mm long, 3–4 mm wide, dorsiventrally compressed, plano-convex, winged, cordate, ciliate on the margins of the upper glume. Upper glume as long as the spikelet, 7(–9)-nerved, winged, with just 3 central nerves reaching the apex, membranous, ciliate, cordate, the apex acute. Lower lemma 3.5–4.4 mm long, 2 mm wide, 3-nerved, glabrous, coriaceous, corrugated and rounded at the base, the margins winged, shortly ciliate. Upper anthecium ellipsoid, 2.8–3.6 mm long, 0.8–1.5 mm wide, plano-convex, papyraceous, pale; upper lemma with simple papillae, bicellular microhairs, and macrohairs toward the apical portion; upper palea with papillae and bicellular microhairs; lodicules 2, ca. 0.4 mm long, hyaline, conduplicate; stamens 3, anthers 1.6 mm long; styles 2, stigma plumose, lateral. Caryopsis obovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic, embryo ½ the length of the caryopsis.

Iconography. Renvoize, Gramíneas de Bolivia: 450, fig. 97. 1998.

Distribution and habitat. Present in Bolivia, in La Paz and Santa Cruz, and Brazil, in the states of Pará, Tocantins, and Mato Grosso. It grows in open fields and "campos rupestres," between 100 and 900 m.

Paspalum reticulinerve is a member of section *Pectinata*, where it is related to *P. aspidiotes* and *P. imbricatum*; the latter has glabrous, solitary spikelets and inflorescences with (2)5 to 7(11) racemes. When describing *P. reticulinerve*, Renvoize (1995) related this species to *P. aspidiotes*, from which this author distinguished *P. reticulinerve* by the densely pubescent, attenuate leaf blades, a ciliate rachis, and smaller spikelets. Later, Renvoize (1998) segregated *P. aspidiotes* from *P. reticulinerve* by having glabrous and cordiform leaf blades, the rachis scabrous, and a smooth upper anthecium. The study of type material of both species, and specimens from Bolivia and Brazil, allowed us to conclude that the real identity of *P. aspidiotes* had been misunderstood: this taxon is clearly separated from *P. reticulinerve* by having solitary spikelets 6.5–7.5 mm long. Also we concluded that the pilosities of leaf blades and inflorescences are unreliable characters to segregate both species: in the specimen *Kuhlmann 1671* the rachis of the racemes is sparsely pilose, with hairs up to 0.4 mm long, while in *Killeen 6541* pilose and attenuated leaf blades are present together with a glabrous rachis of the racemes. A similar situation is present in the specimen *Plowman et al. 8949*, with the rachis of the racemes sparsely pilose.

Representative specimens. BOLIVIA. **Santa Cruz:** Prov. Velasco, Parque Nacional Noel Kempff M., Serranías de Caparuch, *Killeen 6541* (MO); Parque Nacional Noel Kempff M., *Killeen et al. 4824* (SI). BRAZIL. **Mato Grosso:** Serra do Tombador, estrada do Diamantina, *Kuhlmann 1671* (US). **Pará:** Marabá, Serra dos Carajás, *Cavalcante 2131* (US); Mun. Conceição do Araguaia, about 4 km W of town center along hwy. PA-150, *Plowman et al. 8949* (MO, US). **Tocantins:** Mun. Couto Magalhães, Pequizeiro along GO-70, *Plowman et al. 9133* (MO, US).

24. Paspalum stellatum Humboldt & Bonpland ex Flüggé, Gram. Monogr., Paspalum 62. 1810, as "Paspalus stellatus." TYPE: Colombia. Without locality, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (holotype, B-W not seen; isotypes, BM!, US-80051!). Figure 23.

Paspalum stellatum Humb. & Bonpl. ex Flüggé var. *monostachyum* Nees, Fl. Bras. Enum. Pl. 2: 78. 1829, as "Paspalus stellatus var. monostachyus." TYPE: Brazil. Without locality, *F. Sellow 1242* (holotype, M not seen; isotypes, B not seen, P!, US-80052! photo, SI!).

Paspalum stellatum Humb. & Bonpl. ex Flüggé var. *distachyum* Nees, Fl. Bras. Enum. Pl. 2: 78. 1829, as "Paspalus stellatus var. distachyus." TYPE: Brazil. "In apricis arenosis prope Tejuco," *G. H. von Langsdorff s.n.* (holotype, LE not seen).

Paspalum cujabense Trin., Sp. Gram. 3: pl. 284. 1829–1830. TYPE: Brazil. Mato Grosso: Cuiabá, in graminosis humidis, 1829, *G. H. von Langsdorff s.n.* (holotype, LE!; isotypes, K! photo, SI!, US-80050!).

Paspalum wagenerianum Schltdl., Linnaea 26: 13. 133. 1854. TYPE: Venezuela. Distrito Federal: Surfacecas, *Wagener 396* (type not seen).

Paspalum splendens Hack. var. *sphacelatum* Hack., Oesterr. Bot. Z. 51: 239. 1901. TYPE: Brazil. Goiás:

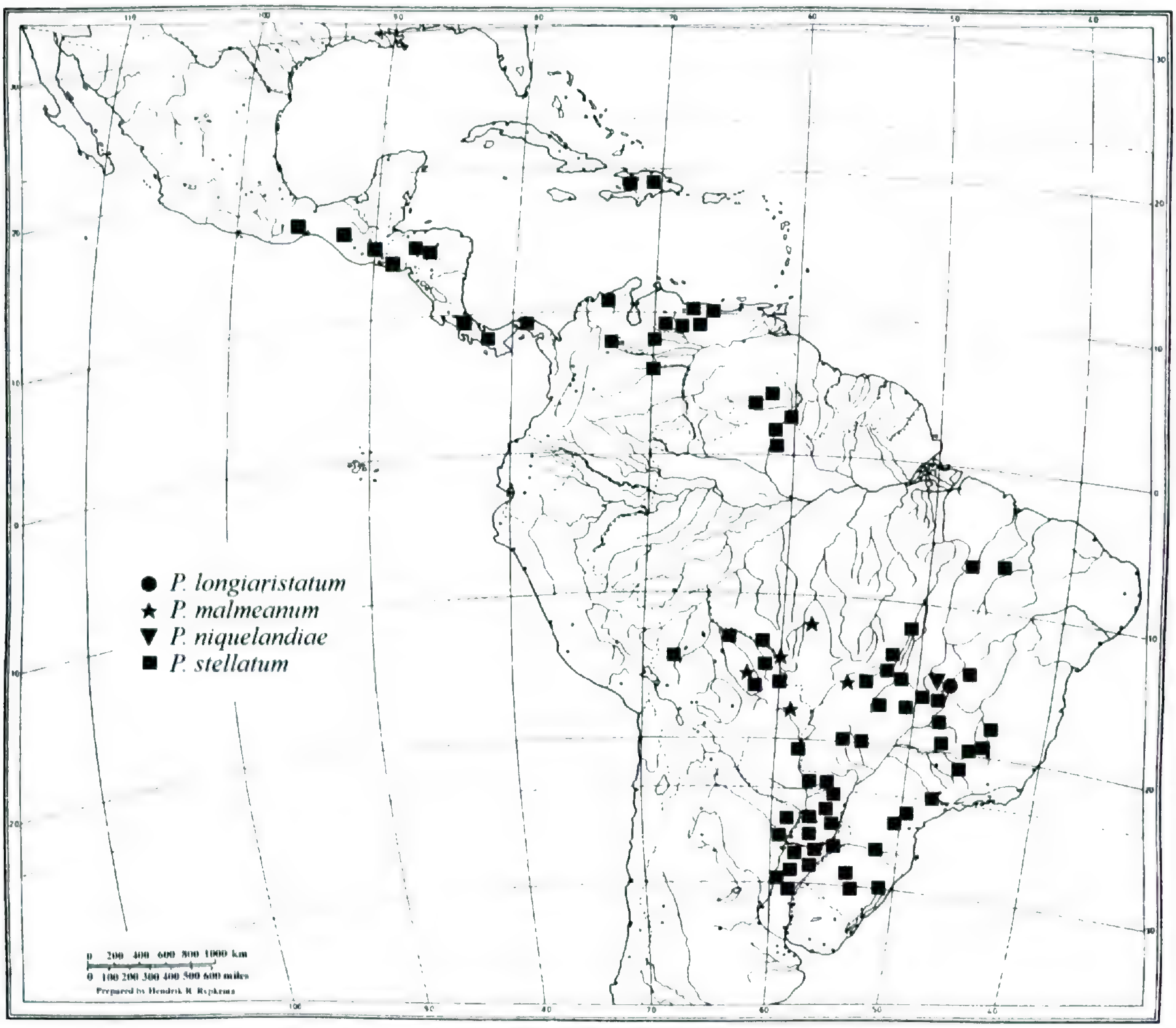

Figure 23. Distribution of *Paspalum longiaristatum*, *P. malmeanum*, *P. niquelandiae*, and *P. stellatum*.

Santa Luzia, 8 Abr. 1895, *A. F. M. Glaziou 22550* (holotype, W!; isotypes, P!, US-2856000!, US-2856001! photo, SI!, US-555446!).

Paspalum stellatum Humb. & Bonpl. ex Flüggé f. *hirsuta* Hack., in Stuck., Anales Mus. Nac. Buenos Aires 21: 28. 1911. TYPE: Argentina. Chaco: Resistencia, 31 Mar. 1908, *H. Mercenaro s.n., leg. T. J. V. Stuckert 18694* (holotype W!; isotypes, CTES!, SI! p.p., US-80049! photo, SI!).

Caespitose, shortly rhizomatous perennial, cataphylls pilose; culms 25–100 cm tall, 0.1–0.2 cm diam., unbranched, erect to geniculate, fasciculate at the base; internodes 3–18 cm long, terete, hollow, glabrous; nodes 3–6, brown, glabrous to shortly pilose. Sheaths 4–8 cm long, striate, glabrous to hirsute, with tuberculate, deciduous hairs, the margins membranous; basal sheaths overlapping. Ligules membranous, short, 0.2 mm long, brown, glabrous; pseudoligule a tuft of short hairs intermixed with long hairs up to 0.5 mm long; collar glabrous. Leaf blades filiform, 8–27 cm long, 0.1–0.3 cm wide, mainly basal, ascendent, rigid, narrowed at the base, apex acuminate, the margins involute, the basal ones ciliate, both surfaces sparsely papillose-hirsute covered with long, tuberculate hairs, or the adaxial surface glabrous. Peduncles up to 25 cm long, glabrous to shortly hirsute. Terminal inflorescences exserted; main axis absent; pulvini shortly pilose, with (1–)2 papyraceous bracts, up to 4 mm long, at the base; racemes 1, rarely 2 conjugated, falcate, ending in a naked point; rachis of the racemes broadly winged, 2–15 cm long, (4–)5–10 mm wide, glabrous to shortly hispid on the adaxial surface, green to purple, midnerve prominent, the margins membranous to hyaline, nerveless, brown, flat to plicate and enclosing the spikelets; pedicels 0.1–0.2 mm long, shortly hirsute, with radiate hairs at the apex; spikelets solitary, arranged in 2 series. Spikelets ovoid to ellipsoid, 2.4–3.9 mm long, 1.2–1.6 mm wide, plano-convex, acute, pale or tinged with purple toward the apex or all over the surface, villous, the upper glume and lower lemma as long as the spikelet. Upper glume membranous, 2–3-

nerved, the central nerves inconspicuous or absent, with a tuft of hairs toward the base, glabrous on the rest of the surface, the margins papillose-pilose, with white hairs up to 4 mm long. Lower lemma glumiform, 2-nerved, the nerves marginal. Upper anthecium narrowly obovoid, 1.8–2.9 mm long, 0.8–1 mm wide, 0.4–1 mm shorter than the upper glume and lower lemma, membranous, pale, smooth, glabrous, shortly stipitate, easily deciduous at maturity; upper lemma 5-nerved, smooth, with sparse bicellular microhairs; lodicules 2, 0.2 mm long; stamens 3, anthers 1.8–2 mm long. Caryopsis obovoid, 1.6 mm long, 0.8 mm wide; hilum elliptic; embryo ½ the length of the caryopsis or slightly shorter.

Iconography. Chase, Contr. U.S. Natl. Herb. 28(1): 16, fig. 1. 1929. Luces de Febres, Las Gramíneas del Distrito Federal: 115, fig. 65. 1963. Burkart, Fl. Il. Entre Ríos: 377, fig. 156. 1969. Rosengurtt et al., Gramíneas uruguayas: 348, fig. 151. 1970. Pohl, Fieldiana, Bot. n.s. 4: 454, fig. 171. 1980. Smith et al., Fl. Il. Catarinense: 922, fig. 185. 1982. Rodríguez, Ernstia 8(2–3): 46. 1998. Renvoize, Gramíneas de Bolivia: 452, fig. 98, D. 1998.

Common name. "Capim-estrela" (Brazil).

Chromosome number. $2n = 32, 52$ (Honfi et al., 1991[1990]); $2n = 20, 32$ (Killeen, 1990).

Distribution and habitat. From southern Mexico, Central America, and the Caribbean to South America, where it is found in Venezuela, Colombia, Bolivia, Brazil, Paraguay, and Argentina; cited for Uruguay by Rosengurtt et al. (1970). It grows in fields or savannas on sandy or rocky soils, or lateritic outcrops, between 0 and 2000 m elevation.

Paspalum stellatum is related to *Paspalum ceresia*, *P. eucomum*, and *P. malmeanum* by its winged and nerveless rachis of the racemes, with spikelets densely pilose. *Paspalum ceresia* differs by its glaucous plants, with filiform to linear-lanceolate leaf blades, 7–21 cm long, 0.3–1.5(–2) cm wide; inflorescences with two to seven racemes (rarely a solitary raceme), alternate, without a bract at the basal pulvini; and pedicels hispidulous and upper anthecium not stipitate. *Paspalum eucomum* is distinguished by having two conjugated racemes (rarely a third one) per inflorescence, rachis of the racemes 1.5–2.5(–4) mm wide, and upper anthecium as long as the upper glume and lower lemma. *Paspalum malmeanum* differs by its rachis of the racemes 1.2–2 mm wide, spikelets 1.6–2 mm long, and upper anthecium as long as the spikelet.

Compound papillae are occasionally present in the upper anthecium of specimens from Santa Cruz, Bolivia.

According to Rosengurtt et al. (1970) and Smith et al. (1982), this species is a low-yield forage grass.

Representative specimens. ARGENTINA. **Chaco:** Dpto. 1° de Mayo, Colonia Benítez, *Schulz 300* (LIL). **Corrientes:** Dpto. Goya, Paraje San Isidro, 46 km S de Goya, *Ahumada et al. 3541* (CTES, K, LIL). **Entre Ríos:** Dpto. Federación, Santa Ana, barrancas del Río Uruguay, *Burkart & Gamerro 21610* (SI). **Formosa:** Dpto. Laishí, without locality, *Joergensen 2882* (G, MO, SI, US). **Misiones:** Dpto. Capital, Posadas, La Granja, *Ekman 594* (US); Dpto. Candelaria, Santa Ana, *Montes 1953* (G, LIL, P, US, W). BOLIVIA. **Beni:** Prov. Iténez, Magdalena, *Moraes et al. 1713* (LPB, SI). **La Paz:** Chaquimayo–Apolo trail ca. 15 km NW of Apolo, *Gentry & Foster 71186* (MO). **Santa Cruz:** Prov. Velasco, San Ignacio, *Beck & Seidel 12330* (MO, SI); Ñuflo de Chávez, Concepción, *Killeen 2474* (MO, SI, US). BRAZIL. **Amazonas:** Uraricuera, *Myers 3404* (US). **Distrito Federal:** Brasília, campus da UNB, *de Jesus 16* (US). **Goiás:** Rio Cristal, 44 km by road SE of Cristalina, *Anderson 8286* (BM, MO, US); without locality, *Glaziou 22546* (G, K, P, W). **Maranhão:** Mun. Loreto, Ilha de Balsas region, *Eiten & Eiten 4417* (K, US). **Mato Grosso:** Mun. Terenos, Faz. Modelo (IPEAO), *Allem & Vieira 2236* (MO); ca. 270 km N of Xavantina, *Ratter et al. 1915* (K, US). **Minas Gerais:** Uberaba, *Chase 12114* (MO, US). **Paraná:** Jaguariaiva, *Dusén 18006* (BM, G, MO, SI). **Rio Grande do Sul:** São Gabriel, *Araujo 345* (US). **Roraima:** Campos Gerais da Região de Caracarahy, *Fróes 23626* (US). **Santa Catarina:** Chapecó, 9 km W of Campo Eré, *Smith & Klein 11529* (US). **São Paulo:** campos d'Ipanema, *Glaziou 13334* (P, US). COLOMBIA. **Arauca:** 13 km al S de Arauca, laguna El Venero, *Joergensen 52* (COL). **Bolívar:** Cerro San Lucas, *Drew E-747* (US). **Boyacá:** Llanos Orientales, El Yopal al S del Hato Matapantano, *Blydenstein & Saravia 1188* (COL). **Magdalena:** Santa Marta, *Smith 142* (BM, K, MO, US). **Meta:** Llanos Orientales, límite de la selva de Arauca, *Blydenstein 736* (COL). **Norte de Santander:** Los Estoraques, La Playa, *Balick 126* (COL). COSTA RICA: **Puntarenas:** 3 km N of the Carretera Interamericana along the road to Boruea, *Pohl et al. 11594* (US). DOMINICAN REPUBLIC. **Dajabón:** Cordillera Central, 6 km de Partido al W en la carretera a Dajabón, *Zanoni et al. 31952* (US). **Monte Cristi:** Sabaneta, Leonor, *Valeur 498* (MO, US). HAITI. Circa Carrajal, *Holdridge 1858* (MO, US). **du Nord:** vicinity of St. Michel de l'Atalaye, *Leonard 7537a* (US). EL SALVADOR. **San Salvador:** Volcán de San Salvador, *Calderón 2272* (US). GUATEMALA. **Jalapa:** between Monjos and Jalapa, about 10 mi. S of Jalapa, *Steyermark 32212* (US). HONDURAS. **Comayagua:** Siguatepeque, *Clewell 3514* (MO). **El Paraíso:** road to Danlí, *Swallen 11226* (MEXU, US). **Francisco Morazán:** 4 km by road SE of Rio Agua Caliente, near Minas de Oro, *Pohl & Gabel 13850* (MO). MEXICO. **Chiapas:** near Caucua, *Nelson 3424* (US); Mun. Villa Corzo, above Colonia Vincente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54586* (MEXU). **Oaxaca:** Distr. Inquila, *Conzali 4364* (MEXU, US). PANAMA. **Coclé:** between Paso de Arado and Olá, *Pittier 5020* (US). **Panamá:** ca. 10 km SW of San Carlos along the Inter-American Hwy., *Davidse & D'Arcy 10126* (MO). **Veraguas:** on Santiago–Santa Fe rd., 18 km S of Santa Fe, *Nee*

8166 (MO). PARAGUAY. **Alto Paraguay:** Fuerte Olimpo, *Anisits 2047* (P). **Amambay:** cerca y al sur de Bellavista, *Fernández Casas & Molero 6335* (G); in regione calcarea cursus superioris fluminis Apa, *Hassler 11058* (BM, G, K, P, US, W). **Caaguazú:** Caaguazú, *Hassler 9259* (BM, G, K, LIL, MO, P, W). **Caazapá:** Tavaí, *Basualdo 2162* (FCQ, MO, SI). **Central:** Tarumandy, *Schinini 6207* (G, LIL, SI, US). **Cordillera:** Barrerito, *Anderson 1120* (US). **Guairá:** Villa Rica, *Joergensen 4568* (BM, MO, SI, US). **Itapúa:** Isla Yaciretá, 6 km de la Ea. Melgarejo, *Quintana et al. 165* (SI). **Misiones:** San Ignacio, *Burkart 18242* (SI). **Paraguarí:** Cerro Peron, prés de Paraguarí, *Balansa 89* (BM, G, K, P, US); Cordillera de Altos, *Fiebrig 664* (BM, G, K, P, SI, US, W). VENEZUELA. **Aragua:** between S. Juan de los Morros and Uberito, *Pittier 11326* (US). **Barinas:** 16 km SW of the Mérida intersection just outside of Barinas, *Davidse 3165* (MO). **Bolívar:** Hato Divina Pastora, *Tamayo 2881* (US). **Carabobo:** Valley of Vijirima, near Guacara, *Pittier 8169* (US). **Cojedes:** 21 km W of San Carlos along Hwy. 5, *Davidse 3140* (MO). **Distrito Federal:** Caracas and vicinity, *Bailey & Bailey 112* (US). **Lara:** Dpto. Palavecino, between the quebrada La Mata and the E side of the Parque Nacional Terepaima, *Burand Jr. & Gantaume V0495* (MO). **Miranda:** Colonia Tovar, *Escalona et al. V274* (MO). **Portuguesa:** Dpto. Guanare, terrenos de la UNELLEZ, *Ramírez 1789* (MO).

25. Paspalum trachycoleon Steudel, Syn. Pl. Glumac. 1: 28. 1855 [1853]. TYPE: Venezuela. Valencia, 9 Oct. 1843, *H. C. Funck 742* (holotype, P!; isotypes, BM!, K!, G!, P!, US-80059!, W!). Figures 24, 25.

Shortly rhizomatous perennial; culms erect to decumbent, (0.8–)1–2 m tall, 0.3–0.6 mm diam., branching at the middle and upper nodes; internodes 5–15 cm long, terete, glabrous, rigid, hollow; nodes pilose to glabrous, brown. Sheaths usually longer than the internodes, overlapping, pubescent to papillose-pilose at the upper portion. Ligules 2–3 mm long, membranous, glabrous; pseudoligule absent. Leaf blades linear-lanceolate, 10–20 cm long, 0.5–1.5 cm wide, flattened, pubescent to papillose-pilose on both surfaces, otherwise glabrous, the base attenuate and the apex acute. Peduncles terminal, partially exserted, pilose. Terminal inflorescences 5–17 cm long, 3–5 cm wide; main axis 3–11 cm long, pilose; racemes 4 to 12, ascendent, divergent, alternate, ending in a naked point; pulvini pilose; rachis of the racemes 3–10 cm long, 4–6 mm wide, foliaceous, green to purple, with a pubescent keel and anastomosed veins on the wings, glabrous, ending in a naked point; pedicels unequal, hispid, laterally inserted in the spikelets; spikelets paired, densely arranged in 4 series. Spikelets ellipsoid, 2.3–3.5 mm long, 1–1.1 mm wide, pale, pilose, with an annular thickening at the base. Upper glume as long as the spikelet, acute to acuminate, hyaline to membranous, the margins pilose with white hairs, a few of them up to 3 mm long, densely pilose toward the base, otherwise glabrous, 3-nerved. Lower lemma as long as the upper glume, acute, membranous, sulcate and with conspicuous nerves, 3-nerved, pilose at the upper portion, otherwise glabrous. Upper anthecium ellipsoid, 2–3.1 mm long, 0.8 mm wide, plano-convex, membranous; upper lemma with simple papillae and bicellular microhairs all over the surface and a tuft of apical macrohairs; upper palea with simple papillae and bicellular microhairs toward the distal portion; lodicules 2, reduced; stamens 3, anthers 1.3–1.4 mm long; stigma plumose. Caryopsis not seen.

Chromosome number. n = 20 (Davidse & Pohl, 1974).

Distribution and habitat. From southern Mexico, Guatemala, Honduras, and El Salvador to Venezuela, Colombia, and central and southern Brazil. It grows in mountain savannas, on dry mountain slopes, between 500 and 2000 m.

Paspalum trachycoleon is close to *P. phyllorhachis* in its similar habit and inflorescence type, which is distinguished by its glabrous spikelets. It is also related to *P. heterotrichon*, but the latter has the rachis of the racemes 3.5–4 mm wide and spikelets solitary.

The specimen *Killip & Smith 19038* has spikelets 3.8–4 mm long.

Representative specimens. BRAZIL. **Distrito Federal:** Reserva Ecológica do IBGE, *da Silva 2659* (MO); near Ribeirão Torto, NE of Lagoa Paranoá, *Irwin et al. 15347* (K, MO). **Goiás:** Niquelândia, *Filgueiras 3567* (SI); without locality, *Burchell 7061-2* (K), *Gardner 4390* (BM, G, K, P). **Minas Gerais:** without locality, *Glaziou 20079* (K). COLOMBIA. **Cundinamarca:** without locality, *without collector 80* (US-1574261). **Huila:** este de Neiva, Cordillera Oriental, *Rusby & Pennell 1014* (US). **Norte de Santander:** Los Estoraques, La Playa, *Balick 127* (COL). **Santander:** Bucaramanga and vicinity, *Killip & Smith 16192* (US); vicinity of Charta, *Killip & Smith 19038* (US). EL SALVADOR. **Copán:** 3 km NW of Copán, *Williams et al. 42957* (US). **San Salvador:** Volcans of San Salvador, *Hitchcock 8946* (US). GUATEMALA. **Zacapa:** slopes of Monte Virgen, *Steyermark 42586* (US). HONDURAS. **El Paraíso:** near 2 km road to Yuscarán, *Swallen 11353* (MEXU, MO, US). **Francisco Morazán:** Rio de Gallo, near El Jicarito, *Swallen 10993* (MEXU, MO, US). **Olancho:** Jutiapa Forest Camp, *Pohl & Gabel 13761* (MO). MEXICO. **Chiapas:** Mun. Cintalapa, 23 km W of Las Cruces along road to La Mina Microwave Station, *Breedlove & Davidse s.n.* (MEXU-830597); Mun. Villa Corzo, above Colonia Vincente Guerrero on road to Finca Cuxtepec, *Breedlove & Davidse 54564* (MEXU). VENEZUELA. **Anzoátegui:** Distr. Libertad, road from El Vigia to Buenos Aires, *Davidse & González 19487* (MO). **Aragua:** de Maracay a Alto, *Croat 21469* (MO). **Distrito Federal:** Caracas, *Bailey & Bailey 447* (US). **Lara:** Distrito Jimenez, entre Alto del Viento y Cerro Pando, *Davidse & González 21162* (SI). **Miranda:** Sebastopol, *Badilla 100*

Figure 24. *Paspalum trachycoleon.*—A. Habit. —B. Detail of ligule. —C. Portion of rachis. —D. Spikelet, dorsal view. —E. Spikelet, ventral view. —F. Upper anthecium, dorsal view. —G. Upper anthecium, ventral view. —H. Caryopsis, scutellar view. —I. Caryopsis, hilum view. (A based on *Davidse & Tillet 4514*, MO; B–I based on *Tamayo 1084*, US.)

Figure 25. Distribution of *Paspalum imbricatum* and *P. trachycoleon.*

(US); San José de Morros, *Davidse & Tillet 4514* (MO). **Monagas:** S-facing mountain slope directly N of Caripe, *Pursell et al. 8580* (US). **Without department:** Barrancas, *Tamayo 1084* (US); Los Venados, *Tamayo 2046* (US).

Excluded Species

Paspalum sanguinolentum Trin. was placed in the subgenus *Ceresia* by Chase (1929), but this species belongs to subgenus *Paspalum*, group Eriantha.

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Appendix 1

List of accepted species of *Paspalum* subg. *Ceresia.*

1. *Paspalum aspidiotes* Trin.
2. *P. biaristatum* Filg. & Davidse
3. *P. buchtienii* Hack.
4. *P. burmanii* Filg., Morrone & Zuloaga
5. *P. cachimboense* Davidse, Morrone & Zuloaga
6. *P. carinatum* Humb. & Bonpl. ex Fluggé
7. *P. ceresia* (Kuntze) Chase
8. *P. cordatum* Hack.
9. *P. cymbiforme* E. Fourn.
10. *P. eucomum* Nees ex Trin.
11. *P. goyasense* Davidse, Morrone & Zuloaga
12. *P. heterotrichon* Trin.
13. *P. humboldtianum* Flüggé
14. *P. imbricatum* Filg.
15. *P. lanciflorum* Trin.
16. *P. longiaristatum* Davidse & Filg.
17. *P. malmeanum* Ekman
18. *P. niquelandiae* Filg.
19. *P. pectinatum* Nees ex Trin.
20. *P. petrense* A. G. Burman
21. *P. phyllorhachis* Hack.
22. *P. polyphyllum* Nees ex Trin.
23. *P. reticulinerve* Renvoize
24. *P. stellatum* Humb. & Bonpl. ex Flüggé
25. *P. trachycoleon* Steud.

Appendix 2

Index to exsiccatae. Each specimen is alphabetically listed by the first collector. The number in parentheses refers to its associated species (see Appendix 1). An asterisk (*) indicates a voucher for the SEM study.

Abraham 83 (6); Acosta Solís 21454 (13); Ahumada 3541 (24); Alba 53–23 (19), 53–96 (6); Allem 1558 (6), 2007 (6), 2236 (24); Almeida 572 (19); Alston 7569 (19); Amat 3 (15); Anderson 1120 (24), 8286 (24), 9413 (22), 9421 (24), 9969 (6), 10304 (22), 35213 (19), 35798 (22); Anisits 2047 (24); Araujo 104 (19), 144 (22), 345 (24); Archer 629 (13), 3843 (24), 4995 (22); Arechavaleta s.n. (22); Argent 6460 (22), 6766 (19); Aristeguieta 238 (25), 4219 (6); Arsène 2813 (13); Asplund 6531 (13), 7593 (13), 10498 (13), 10633 (19), 12014 (13); Aynard 6019 (6).

Badilla 100 (25); Bailey 112 (24), 447 (25); Balansa 89 (24), 90 (22), 90a (22), 126 (24), 127 (25); Balick 127 (25); Balls 6923 (13); Bang 265 (3); Barbosa 3018 (19), 3032 (19); Barclay 5703 (13); Barlow 30/1173 (19); Barreto 46 (24), 529 (22), 1483 (22), 1577 (24), 2952 (19); Basualdo 2162 (24); Beck 4025 (7), 8714 (3), 12330 (24), 19948 (3), 20552 (19), 20564 (6); Bentacur 1510 (19); Berro 2680 (22); Bertoni 5406 (24); Black 47–1777 (6), 51–12029 (19), 51–12148 (22), 51–12291 (6); Blake 7445 (19); Blydenstein 734 (19), 736 (24), 847 (6), 856 (19), 900 (19), 939 (8), 1037 (19), 1082 (6), 1188 (24), 1468 (15), 1562 (19); Boelcke 16646 (13); Borges 189 (22); Brade 19638 (8), 20377 (22); Breedlove 3313 (13), 13822 (9), 20498 (9), 39106 (9), 42481 (25), 53954 (24), 54362 (12), 54468 (25), 54564 (25), 54586 (24), 54596 (12), s.n. (25); Brooks 70 (24), 125 (7), 144 (16); Bruderreck 2 (6); Buchtien 447 (3), 3629 (3), 4274 (3), s.n. (3); Burandt, Jr. V0495 (24), V0530 (12); Burchell 4329 (22), 4574 (22), 4681 (22), 5769 (22), 7061–2 (25), 7124 (25), 7295 (25); Burkart 5335 (13), 10211 (13), 11014 (13), 16984 (13), 18242 (24), 21610 (24); Burman 393 (24).

Caballero Pardo 77 (7); Cabrera 2278 (8), 22730 (7), 28254 (24); Calderón 2272 (24), 2708 (8), 2760 (1); Callejas 6886 (15); Calzada 17051 (19); Camp E-2743 (13), 2332 (7); Capell s.n. (22); Cárdenas 515 (13), 3410 (13), 3606 (22); Carnevali 1083 (24), 3124 (24), 3200 (22), 3379 (24); Castellanos 17922 (22), 17957 (22); Cavalcante 2131 (23); Chase 1239 (24), 8337 (22), 8975 (21), 9100 (24), 9148 (22), 9212 (19), 9250 (19), 9253 (24), 9295 (24), 9308 (24), 9325 (21), 9352 (22), 9367 (22), 9369 (22), 9559 (22), 9917 (22), 10230 (19), 10249 (19), 10276 (19), 10306 (6), 10350 (19), 10595 (6), 10655 (19), 10740 (22), 10872 (24), 10907 (24), 11200 (10), 11543 (24), 11549 (22), 11602 (22), 11768 (24), 11962 (17), 12014 (24), 12028 (24), 12085 (25), 12088 (24), 12114 (24), 12292 (25), 12294 (13); Chávez 3217 (7); Chaviel 450 (1); Claussen s.n. (24); Clayton 4631 (8), 4804 (6); Clewell 3514 (24); Conzali 4364 (24); Coradin 696 (6); Costa Sacco 133 (22); Croat 21469 (25); Cuatrecasas 3001 (13), 7649-A (19), 25702 (13).

D'Arcy 141 (22), 2271 (22), 2659 (25), 4082 (6), 13527 (15); Daly 2171 (22); Daniel A-2 (19), 60 (6); Davidse 3065 (25), 3082 (12), 3140 (24), 3165 (24), 4073 (13), 4514 (25), 4615a (6), 4708 (1), 5109 (19), 5242 (19), 5321 (19), 5597 (13), 10126 (24), 10655 (22), 10967 (22), 10985 (22), 11028 (22), 11123 (22), 11148 (22), 11308 (22), 11316 (22), 11380 (22), 11401 (22), 11407 (22), 12087 (6), 12124 (6), 12158 (25), 12159 (24), 12276 (24), 14176 (19), 15652 (19), 16117 (19), 16775 (6), 16942 (6), 18355 (6), 19314 (15), 19317 (6), 19487 (25), 19802 (6), 20544 (19), 21162 (25), 21312 (25), 21370 (13), 22647 (15), 22944 (1), 28159 (13), 31637 (9), 35448 (13); Dawson 14142 (24), 14215 (24), 14863 (25); de Campos 192 (22); de Jesus 3 (10), 16 (24); de Lima s.n. (22); de Paula 65 (24); Dedecca 302 (22); Dias 67 (10); Dinelli 12876 (7); Dombrowski 780 (19), 4570 (22), 5984 (22), 6488 (19), 6715 (19), 9037 (19), 9784 (19); Drew E-747 (24); Dusén 26a (22), 283 (22), 2770 (19), 2844 (19), 2844a (19), 3657 (22), 3659 (22), 4023 (24), 8011 (24), 9109 (8), 10412 (6), 10611 (19), 10613 (19), 13256 (19), 13805a (22), 14489 (22), 15727 (19), 16057* (19), 16174 (8), 17388a (22), 17407 (19), 17934 (6), 18006 (24), 18065 (10), s.n. (22); Dutra 464 (22).

Echeverry 1251 (13), 2312 (15); Eggler 639 (9); Egler 1262 (15); Eiten 3777 (7), 4417 (24), 4418 (7), 6746 (19), 6760 (19), 7626 (22), 9151 (19); Ekman 594 (24), 596 (24), 2274 (12), 2302 (24), 2401 (12), 2484 (24), 13404 (12), 14018 (12); Ellenberger 1369 (22); Enamorado 23 (9); Escalona V274 (24); Eskuche 4556 (22).

Fassett 25502 (13); Felippone 6462 (22); Fendler 1697 (25), 1698 (12), 2533 (24); Fernández 89 (24); Fernández Casas 6335 (24); Ferreyra 5373 (13); Fiebrig 664 (24), 2664 (7), 3082 (13), 4970 (24), 4978 (24), 6222 (22); Filgueiras 2131 (14), 2184 (14), 2280 (7), 2342 (16), 2408 (2), 2409 (2), 2455 (19), 2477 (4), 2780 (16), 3260 (22), 3392 (16), 3317 (14), 3567* (25); Filipovich 398 (13);

Flores Flanco 3643 (13); Fonseça 224 (2), 227 (16), 600 (22); Fontana 114–5 (24); Fraser 370 (1); Freytag s.n. (24); Fróes 23626 (24); Funcke 742 (25).

García Barriga 4993 (19), 21426 (15); Gardner 4030 (24), 4390 (25); Gentry 15081 (19), 71186 (24); Gifford G-101 (15); Giraldo-Cañas 2566 (6), 2631 (19); Glaziou 2260 (22), 4309 (22), 6775 (22), 7980 (22), 13334 (24), 16548 (22), 17406 (10), 17410 (22), 17411 (22), 17414 (24), 17940 (22), 18607 (22), 18644 (22), 18674 (22), 20070 (21), 20076 (21), 20078 (21), 20079 (25), 20082 (22), 20083 (22), 20084 (15), 22427 (19), 22437 (22), 22441 (11), 22443 (11), 22544 (15), 22544b (14), 22545 (24), 22546 (24), 22547 (6), 22549 (24), 22551 (10), 22553 p.p. (24), 22555 (10), 22556 (6), 22557 (24), 22558 (22), 22559 (22), 22560 (22), 22561 (22), 22562 (22), 22576 (12), 22577 (25), 22949 (24), s.n. (24); Goés s.n. (22); Goodland 923 (15); Gottsberger 1043 (10); Graham 520 (19); Grignon 84257 (13); Guala 1320 (24), 1450 (22); Guánchez 3618 (1); Gutiérrez 655 (17).

Haase 630 (19); Hahn 5592b (15); Handro 97 (22); Harley 10330 (19), 10480 (19), SH209 (22); Hassler 1039 (24), 1058 (24), 9259 (24), 9261 (22), 9261a (22), 9380 (22), 10209 (22), 11058 (24), 11501 (22), 11561 (22), 11916 (22); Hatschbach 5461 (22), 6864 (22), 7751 (22), 8965 (22), 11110 (22), 12097 (8), 16134 (22), 25048 (19), 25264 (19), 32479 (19), 33152 (19), 44562 (22), 45697 (19), 47650 (24), 48811 (19), 64890 (22), 66698 (22); Haught 2709 (19); Hazlett 994 (24); Heithaus 163 (19); Heringer 4615 (15), 7249 (22), 7382 (14), 10432 (22); Hermann 10995 (19), 11089 (19); Hernández 2283 (19); Hernández Xolocotzi X-623 (12); Herter 1755 (22); Heyde 6271 (13); Hicken s.n. (24); Hill 1548 (19); Hinton 1440 (13), 2532 (9), 11400 (13); Hitchcock 6355 (13), 6837 (13), 7055 (13), 7297 (13), 8186 (13), 8297 (12), 8946 (25), 21306 (13), 21710 (13), 22830 (13); Holdridge 1858 (24); Holway 98 (22), 1633 (22), 1672 (22), 1708 (24); Hostmann 1306 (6); Huber 9643 (1), 9898 (1); Hunt 5550 (24), 6012 (22), 6246 (22); Hutchinson 4495 (13), 5194 (7).

Ibarrola 2834 (24); Idrobo 11636 (13); Iltis 342 (13); Imaguire 605 (22); Irwin 739 (6), 5163 (24), 5171 (22), 5647 (22), 5800 (22), 6205 (22), 6579 (19), 6758 (19), 6806 (19), 7069 (22), 7219 (22), 8001 (24), 9495 (22), 9648 (11), 9658 (11), 10044 (22), 10257 (11), 10654 (11), 10737 (11), 13034 (14), 13241 (14), 15177 (24), 15328 (10), 15347 (25), 15928 (24), 15929 (24), 16232 (22), 16232a (22), 16465 (24), 17256 (22), 17314 (24), 17617 (24), 17854 (22), 17967 (22), 19486 (22), 27667 (6), 28353 (22); Isabell s.n. (7).

Jangoux 10153 (19); Joergensen 1765 (13), 2882 (24), 4568 (24); Joly 1456 (24); Jorgensen 52 (24); Jürgens G-299 (22).

Killeen 687 (24), 904 (24), 1795 (22), 1952 (24), 1998 (24), 2011B (24), 2024* (17), 2076 (17), 2458 (24), 2473 (24), 2474* (24), 2477 (24), 2478 (17), 2487 (24), 2782a (19), 2795 (22), 2823 (6), 4152 (7), 4824 (23), 4929 (15), 6056 (24), 6541 (23); Killip 4555 (12), 16192 (25), 19038 (25), 19770 (13), 34321 (19); Klein 3916 (19); Koninck 157 (25); Kral 69245 (19), 72050 (1), 75939 (11); Krapovickas 14972 (24), 25202 (24); Kuhlmann 1667 (17), 1668 (17), 1671 (23), 1674 (15), s.n. (22); Kummrow 2204 (22).

Lazor 3350 (19); Leavenworth 1649 (13); Lehmann 979 (19); Leonard 7526 (24), 7537a (24), 7793 (12), 8953 (12), 8957 (12); Liebmann 225 (9); Liesner 19350 (15); Lima 58–3056 (24); Linares 3663 (9), 3904 (9); Linden 1555 (25); Llano 47 (6); Llatas Quiroz 2322 (13); Loefgren 2331 (22).

Macedo 351 (10), 1121 (12), 1543 (8); Machado de Campos 111 (19); Machuca Nuñez 4640 (13); Magalhães 101 (22), 908 (21), 19226 (24); Maguire 32038 (15); Malme 965 (22), 1562b (12), 2226 (22), s.n. (22); Mandon 1254 (13); Marin 851 (13); Martius 267 (22); Martínez F-1953B (13); McVaugh 19098 (13); Mendoça 2293 (22); Mereles 2943 (24); Mexía 5519 (24); Meyer 2090 (22), s.n. (24); Miranda 3883 (24); Molina 8702 (25), 12041 (13), 13177 (24); Montes 1943 (22), 1953 (24), 1959 (22), 14920 (24), 15353 (24), 16250 (24), 16409 (24), 27642 (24); Montoro s.n. (22); Moraes 1713 (24); Moran 5505 (12); Mori 13303 (22), 17298 (6); Moritz 1537 (25); Morrone 205 (24); Mostacedo 314 (7), 1783 (23), 1862 (1); Müller 2036 (13); Mutis 5453 (19), 5537 (13); Myers 3338 (19), 3404 (24).

Nee 8166 (24), 26848 (3), 40372 (7), 46904 (19), 49412 (22); Nelson 3424 (24); Nicora 4700 (22), 4708 (24), 6352 (24); Niederlein 570 (22); Norrmann 159 (24); Núñez 7175 (13).

Oldenburger 5 (15); Oliveira 305 (7), 598 (7), 615 (2), 623 (2), 630 (2), 638 (16), 700 (16), 719 (12), 758* (2), 763 (19); Øllgaard 90721 (7); Orozco 182 (19); Orth 1059 (22); Osten 6632 (22).

Parodi 2412 (22), 4664 (24), 7070 (24); Partch 69–91 (13); Pedersen 1032 (22), 2611 (24), 3783 (24), 11677 (22), 13371 (22), 15713 (24); Pennell 8174 (19); Perdonnet 496 (22); Peterson 9478 (7), 11887 (22), 11891 (24); Pinheiro 142 (7), 517 (7), 625 (7); Pinto 796 (19), 894 (19), 1066 (19), 1141 (19), 1467 (19), 1550 (19); Pire 14649 (24); Pires 2290 (24), 16684 (24); Pittier 214 (25), 1788 (25), 4351 (19), 5020 (24), 5902 (25), 6033 (25), 7487 (24), 7489 (24), 8169 (24), 9734 (13), 11326 (24), 11998 (24), 12818 (25); Plowman 8949 (23), 9133 (23), 19132 (15); Pohl 714 (19), 1454 (15), 2833 (24), 11594 (24), 12274 (6), 12361 (19), 13531 (9), 13761 (25), 13850 (24), 13922 (19); Porter 4300 (19); Prance 13823 (1); Purpus 2002 (13); Purseglove 6514 (6); Pursell 8580 (25).

Quarín 2235 (24), 3340 (24), 3716 (24), 3852 (24), 4043 (24); Quintana 165 (24); Quiroga 38 (24).

Rambo 40511 (22), 40690 (22), 40804 (22), 53906 (22), 54017 (22), 54991 (22); Ramia 1009 (24); Ramirez 961 (15), 1789 (24); Ramos 182a (6); Ratter 520 (22), 820 (24), 1915 (24), 1969 (19), 2883 (24), 2884 (25), 3335 (24); Reeder 3313 (13); Reeves 194 (25); Regnell III-1345 (25), III-1344 (24), III-1335 (19), I-466 (22); Reineck 431 (22); Reitz 10652 (22), 10659 (22), 10681 (22), 10906 (22), 10933 (22), 12477 (22); Renvoize 3870 (7), 4038 (13), 4048 (22), 5409 (19); Riedel 966 (12), 1043 (22), 1048 (1), 2143 (22), s.n. (1), s.n. (12), s.n. (19), s.n. (22), s.n. (24); Rivera L-L41 (19), 3 (19); Rizzo 4285 (22); Robinson 3189 (22); Rodrigues 662 (6); Rodríguez 206 (24); Rojas 2757 (24), 9569 (22), 13404 (22), 13933 (22); Romanczuk 112 (24); Rombouts 308 (19); Rondon 2135 (6), s.n. (15), s.n. (24); Rosengurtt B-3197 (22), B-5749 (24), B-5750 (22), B-5883 (24), B-7397 (22); Rueda 1200 (9); Rusby 1014 (25); Rzedowski 17636 (13).

Sánchez Vega 2332 (7), 2341 (13); Santos 1701 (24); Saravia 4006 (13), 4186 (22), 4215 (22), 12315 (22); Schaffner 120 (13), 154 (13); Schenck 3155 (22); Schinini 1323 (24), 1403 (24), 1436 (24), 6207 (24); Schmidt 53 (22), 136 (13); Schreiter 9251 (13), 9256 (7); Schulz 300 (24), 7220 (24), 17275 (22); Schwacke 8444 (22); Schwarz 2214 (22), 5539 (24), 5703 (24), 10003 (24), 10161 (24); Sellow 1232 (19), 1239 (19), 1240 (22), 4416 (22), 5686 (24), s.n. (19), s.n. (22), s.n. (24); Semir 380 (19); Semple

150 (19); Sendulsky 1239 (10); Sermeño s.n. (13); Shaw s.n. (19), s.n. (6); Silva 114 (24); Smith 142 (24), 143 (12), 2170 (25), 5907 (22), 6316 (22), 6912 (24), 8445 (19), 11529 (24), 12013 (22), 12106 (22), 14462 (6), 14579 (8), 14858 (8), 15569 (19), 16123 (22); Soderstrom 1124 (6); Sohns 427 (13); Soria 4442 (24); Soriano 986 (13); Souza 5548 (7); Spegazzini s.n. (22); Standley 13185 (12), 56275 (24); Steinbach 3015 (3), 3712 (22), 5162 (22), 5385 (22), 6618 (13), 6808 (22), 7103 (24); Stevens 24761 (13), 25701 (13); Steyermark 29550 (9), 32312 (24), 42586 (25), 55152 (25), 59150 (19), 75259 (19), 121984 (25), 127710 (24), 127714 (25); Stockwell 893 (13); Stuckert 14159 (13), 18694 (22); Swallen 3074 (19), 3643 (6), 3687 (6), 3772 (7), 4029 (15), 4078 (6), 4762 (6), 8344 (19), 8361 (22), 8477 (19), 8486 (22), 8518 (22), 8584 (22), 8613 (22), 8639 (22), 8698 (22), 8772 (22), 8784 (22), 8932 (22), 8975 1/2 (22), 8994 (22), 9033 (22), 9083 (22), 9087 (22), 9132 (22), 9150 (22), 9159 (22), 9181 (22), 9540 (24), 9590 (24), 10747 (9), 10809 (9), 10810 (12), 10993 (25), 11226 (24), 11353 (25), 11354 (12), 11401 (12).

Tablas 738 (13); Tamayo 1084 (25), 1867 (22), 2046* (25), 2281 (13), 2881 (24), 3198 (15), s.n. (15); Tate 157 (15); Tenorio 16710 (13); Texeira 1197 (1); Torrico 331 (7); Tovar 1005 (13), 1020 (7), 4176* (12); Triana 761 (25); Troncoso 3387 (24).

Ule 7919 (24), 8032 (24).

Valeur 498 (24); Valls 8340 (6); van der Werff 7863 (22); Vargas 2459 (7), 19047 (7); Venturi 8320 (7), 9905 (7); Vieira 54 (22); Villa Carenzo 1818 (13); Vincelli 1146 (19).

Warming s.n. (25); Webster 29732 (19); Weddell 1699* (8), 2556 (10); Widgren s.n. (22), s.n. (19); Williams 10533 (24), 13088 (15), 14704 (24), 17344 (24), 42957 (25); Wood 4273 (22), 4306 (25), 7852 (13); Wurdack 27 (15).

Zardini 26848 (24), 51117 (19); Zanoni 31952 (24); Zuloaga 888 (22), 910 (24), 2383 (22), 3835 (11), 3839 (19), 4379 (6), 4413 (15), 4587 (22), 4606 (22), 4654 (22), 4697 (22), 4874 (22), 4904 (22), 4930 (22), 5371 (24), 5671 (24), 5788 (24), 5791 (22), 5885 (13), 6585 (22), 6817 (24), 6944 (22).

Appendix 3

List of specimens for outgroup taxa in the cladistic analysis.

Anthaenantiopsis fiebrigii L. Parodi
ARGENTINA. **Jujuy:** Dpto. Dr. M. Belgrano, Zapla, Mina 9 de Octubre, *Cabrera et al. 32666* (SI).
Panicum
Panicum laxum Sw.
ARGENTINA. **Corrientes:** Monte Caseros, monte del arroyo El Seibo, *Nicora 4516* (SI). **Misiones:** Dep. Iguazú, Cataratas Iguazú, *Cabrera et al. 28942* (SI). **Santa Fe:** Río Paraná, Canal Viejo, *Job 710* (SI).
Panicum obtusum Kunth
U.S.A. **Arizona:** Box Canyon Road, *Gould 2889* (SI).
Paspalum Group Dissecta
Paspalum acuminatum Raddi
ARGENTINA. **Tucumán:** Dpto. Monteros, Loc. Monteros, *Lillo 38377* (SI); Dpto. Leales, Loc. Leales, *Venturi 699* (SI). **Entre Ríos:** Dpto. Feliciano, río Guayquiraró, Ruta 12, *Burkart et al. 23250* (SI).
Paspalum dissectum (L.) L.
U.S.A. **Alabama:** N side of Gulf Shores, *Kral 51314* (MO). **Louisiana:** Cheniere Lake, *Burkunas 605* (MO).
Paspalum Group Eriantha
Paspalum erianthum Nees ex Trin.
BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, Est. Las Madres, *Killeen 1369* (SI). BRAZIL. **Distrito Federal:** Area da Proflora, *Filgueiras & Zuloaga 2207* (SI); Brasília, Lago Sul, *Zuloaga 3836* (SI)
Paspalum guttatum Trin.
BRAZIL. **Distrito Federal:** between Brasília & Sobradinho, *Irwin et al. 9163* (MO). **Goiás:** s.l., *Glaziou 22442* (G).
Paspalum sanguinolentum Trin.
BRAZIL. **Goiás:** 3 km of Cristalina, *Irwin et al. 9858* (MO). **Minas Gerais:** Sierra da Piedade, Santuario, *Zuloaga & Morrone 4676* (SI).
Paspalum Group Notata
Paspalum almum Chase
PARAGUAY. **Central:** Tavarory, 3 km S from administration, 1 km E of río Paraguay, *Zardini & Tillería 29180* (SI); Itá Enramada, *Schinini 6277* (SI). **Pte. Hayes:** Estero Patiño, ruta Trans Chaco, km 164, *Quarín 4049* (SI).
Paspalum cromyorrhizon Trin. ex Döll
ARGENTINA. **Corrientes:** orillas del Timboí, camino de Monte Caseros, *Nicora 4629* (SI). BRAZIL. **Río Grande do Sul:** Centro Agronómico de Guaiba, *Burkart 25051* (SI). URUGUAY. **Durazno:** La Paloma, *Schroeder s.n.* (SI).
Paspalum notatum Flüggé
ARGENTINA. **Córdoba:** Santa María, Alta Gracia, *Hunziker 1178* (SI). **Corrientes:** San Miguel, 19 km S de Caa-Catí, Ruta 5, *Ahumada 1837* (SI); Monte Caseros, orillas del Uruguay, *Nicora 4587* (SI). **Misiones:** Dpto. Apóstoles, Apóstoles, *Burkart 14273* (SI).
Paspalum Group Racemosa
Paspalum candidum (Humb. & Bonpl. ex Flüggé) Kunth
ARGENTINA. **Jujuy:** Dpto. Dr. Manuel Belgrano, faldeo del Cerro Sendero Abra de Lozano, *Deginani & Cialdella 135* (SI); Dpto. Capital, Lagunas de Yala, *Cabrera et al. 30676* (SI); Termas de Reyes, *Burkart et al. 11218* (SI).
Paspalum prostatum Scribn. & Merr.
MEXICO. **Hidalgo:** near Honey Station, *Pringle 8891* (SI). VENEZUELA. **Lara:** Distrito Jiménez, 4–5 km of Sanare, *Davidse & González 21366* (SI).
Paspalum racemosum Lam.
PERU. **Lima:** Chancay, Lomas of Pasomayo, S of Chancay, *Stork & Vargas 9344* (SI). **Trujillo:** La Libertad, Cerro Cabezón, *Sagástegui & Mostacero 10443* (SI); La Libertad, Barraza, *Mostacero & Ramírez 690* (SI).

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PHYLOGENY OF THE TRIBE HYMENOCALLIDEAE (AMARYLLIDACEAE) BASED ON MORPHOLOGY AND MOLECULAR CHARACTERS[1]

Alan W. Meerow,[2] Charles L. Guy,[3] Qin-Bao Li,[3] and Jason R. Clayton[4]

Abstract

The generic limits of *Hymenocallis* have been variously proposed by different taxonomic workers, often without discussion or data. The genera *Leptochiton*, *Ismene*, *Elisena*, and *Pseudostenomesson* have been included with *Hymenocallis*, lumped together as the genus *Ismene*, or maintained as distinct genera. Recent cladistic analysis of plastid and nrDNA for Amaryllidaceae support a distinct tribe Hymenocallideae. Cladistic analyses of morphology, and plastid (*trn*L-F region) and nuclear ribosomal DNA (ITS) are presented alone and in combination for the tribe. *Leptochiton* is sister to the rest of the genera in the tribe in all analyses. While *Hymenocallis* is always resolved as monophyletic, *Ismene* is variably paraphyletic or monophyletic. The combined sequence data produce the most resolved and best-supported phylogeny, wherein *Hymenocallis* and *Ismene* are monophyletic sister genera. These data support an origin for the tribe in the Andes, with vicariant distribution of the largely Mesoamerican *Hymenocallis*. Formal recognition of *Ismene* subg. *Elisena* and *Pseudostenomesson* is established.

Key words: Amaryllidaceae, cladistics, molecular systematics, phylogeny.

Systematics of the genus *Hymenocallis* Salisb. (Amaryllidaceae) and its allies have defied precise systematic understanding at both the specific and generic levels (Flory, 1976; Meerow & Dehgan, 1985). The genera *Hymenocallis* and *Ismene* Salisb. were established by Salisbury (1812) for the Neotropical species with fleshy seeds originally assigned to the Old World genus *Pancratium* L. The zygomorphic-flowered *Elisena* was described by Herbert (1837), who recognized *Hymenocallis* and *Ismene* as distinct genera. Baker (1888) subsumed *Ismene* within *Hymenocallis* but retained *Elisena* as distinct, as did Pax (1890). While Stapf (1933) treated *H. quitoensis* Herb. as a species of *Pamianthe* Stapf, Sealy (1937) considered the species to exhibit sufficient morphological divergence to be recognized as a monotypic genus, *Leptochiton* Sealy. Hutchinson (1934, 1959) retained both *Elisena* and *Ismene* (presumably including *Leptochiton*) as distinct. Velarde (1949) established the Peruvian genus *Pseudostenomesson* for a fleshy-seeded species originally described as *Stenomesson morissonii* Vargas as well as one new species. Traub (1962) recognized all four erstwhile genera as subgenera of *Hymenocallis* in his synoptic treatment: subg. *Hymenocallis*, subg. *Ismene* (Salisb.) Baker ex Traub (including *Leptochiton*), subg. *Elisena* (Herb.) Traub, and subg. *Pseudostenomesson* (Velarde) Traub. Traub (1980) later reduced these subgenera to the rank of section without explanation. Ravenna (1980) in his description of *H. heliantha* (= *Leptochiton heliantha* (Ravenna) Gereau & Meerow) suggested that subgenera *Ismene* (including *Lepidochiton*), *Elisena*, and *Pseudostenomesson* should probably be all recognized as the genus *Ismene*, distinct from *Hymenocallis*. Meerow and Dehgan (1985) suggested that *Pseudostenomesson* might warrant recognition at the rank of genus due to its extreme phenetic divergence (funnelform-tubular perianth) versus the "pancratioid" flower of *Leptochiton*, *Ismene* subg. *Ismene*, and *Hymenocallis*. "Pancratoid" floral morphology refers to a large, white, fragrant, crateriform flower with a conspicuous staminal cup (cf. *Pancratium* L.). This type of flower appears to be adapted for sphingid moth pollination (Bauml, 1979; Grant, 1983; Morton, 1965). Meerow (1990) treated *Leptochiton* as a distinct genus and recognized *Hymenocallis* and *Ismene* (including *Elisena* and *Pseudostenomesson*) as distinct, a treatment followed by Gereau et al. (1993) and

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Meerow and Snijman (1998). No cladistic analysis has focused exclusively on testing the validity of this treatment, although at least one representative of each subgenus was included in overall molecular studies of Amaryllidaceae (Meerow et al., 1999, 2000a).

Hymenocallis and its allied segregate genera are entirely Neotropical in distribution [a single West African taxon, *H. senegambica*, was treated by Sealy (1954) as an early adventive introduction of *H. caribaea*]. *Hymenocallis* sensu stricto, with 50 to 60 species, is chiefly Mesoamerican and extends into the West Indies and the southeastern United States. It is sparingly represented in northern South America. *Leptochiton* Sealy (2 spp.), *Ismene* (ca. 7 spp.), *Elisena* Herb. (2 to 4 spp.), and *Pseudostenomesson* Velarde (2 spp.) are all endemic to the Central Andean region of South America. *Hymenocallis*, *Ismene*, and *Leptochiton* are contrasted in Table 1.

Hymenocallis and allies have usually been allied with *Eucharis* Planch. in the tribe Euchardeae (Hutchinson, 1934, 1959; Traub, 1963; Dahlgren et al., 1985; Müller-Doblies & Müller-Doblies, 1996). Meerow (1989, 1995) argued that the linkage of these genera, largely through the perception that both lineages shared a fleshy seed, was misconstrued, and proposed that either subtribal or tribal recognition of *Hymenocallis* and allies was warranted. Müller-Doblies and Müller-Doblies (1996) placed them in Euchardeae subtribe Hymenocallidinae, while Meerow and Snijman (1998) recognized a distinct tribe, Hymenocallideae. Family-wide analysis of plastid sequences (Meerow et al., 1999) and nrDNA analyses of the monophyletic American clade of the family (Meerow et al., 2000a) support a distinct Hymenocallideae as sister to the newly recognized tribe Clinantheae (a segregate of the former Stenomesseae), but complete resolution of the intratribal relationships is not apparent in these large analyses. Both tribes are subclades of a well-supported, Andean, tetraploid clade of genera.

In this paper, we present phylogenetic analyses of morphological and molecular data for the tribe Hymenocallideae, and seek to clarify the relationships within the tribe.

Materials and Methods

Sampling

Sequences for the plastid *trn*L-F region were newly obtained for *H. eucharidifolia*, which, along with *H. latifolia*, was used as an exemplar taxon of *Hymenocallis* (Table 2). Previously cited sequences were used for one species each of the three subgenera of *Ismene*, one species of *Leptochiton*, and the outgroup *Pamianthe peruviana* (Table 2, Meerow et al., 1999). For ITS and the morphological data matrix, we increased our sampling with an additional four species of *Hymenocallis* and two additional species of *Ismene* subg. *Ismene* (Table 2). The aligned sequence matrices are available from the first author (miaam@ars-grin.gov).

Morphological data

Morphological and cytological character state data were derived from the following sources: Traub (1962, 1980), Sealy (1954), Flory (1976), Velarde (1949), Bauml (1979), Meerow and Dehgan (1985); from examination of living material in research collections at the USDA, Miami, Florida; field observations of *Hymenocallis*, *Ismene*, and *Leptochiton* species; and examination of herbarium material. The morphological matrix consists of 12 species representing 4 genera and 23 characters (Tables 3, 4).

Sequence data

The *trn*L-F (*trn*L intron and spacer region between *trn*L and *trn*F) matrix consisted of 6 taxa and 906 base positions. The nrDNA ITS sequence matrix (ITS1, 5.8s intron, ITS2) consisted of 12 taxa and 636 bp.

DNA extraction, amplification, and sequencing protocols

Genomic DNA was extracted from silica gel dried leaf tissue as described by Meerow et al. (2000a). The *trn*L-*trn*F region was amplified using the primers of Taberlet et al. (1991) as described by Meerow et al. (1999). Amplification of the ribosomal DNA ITS1/5.8S/ITS2 region was accomplished using flanking primers (18S, 26S) AB101 and AB102 (Douzery et al., 1999), and the original White et al. (1990) internal primers ITS2 and 3 to amplify the spacers along with the intervening 5.8S sequence, as described by Meerow et al. (2000a). Amplified products were purified using QIAquick (Qiagen, Valencia, California) columns, following manufacturer's protocols. All polymerase chain reactions (PCR) were performed on an ABI 9700 (Applied Biosystems, Foster City, California).

Cycle sequencing reactions were performed directly on purified PCR products on the ABI 9700, using standard dideoxy cycle protocols for sequencing with dye terminators on either an ABI 377 or ABI 310 automated sequencer (according to the manufacturer's protocols; Applied Biosystems, Foster City, California).

Table 1. Comparison of the genera and subgenera of Amaryllidaceae tribe Hymenocallideae.

Genus or subgenus	Number of species	Distribution	Elongate pseudostem	Floral morphology	Ovules per locule	Phytomelan on seed coat	Chromosome number
Leptochiton	2	SW Ecuador and NW Peru, at low elevations	Absent	Pancratioid, actinomorphic, large, white or yellow, fragrant, sessile, (sub)erect; tube long; staminal cup large and striped green within; free filament short and incurved.	16–20	Present	$2n = 34$
Ismene subg. *Ismene*	5–7	Central Andes at low to high elevations	Present	Pancratioid, actinomorphic large, white or yellow, fragrant, 2–10, subsessile to pedicellate, horizontal or declinate, tube ± long, staminal cup large, striped green within; free filament short and incurved.	2–4	Absent	$2n = 23$–86, 46, 104–110
Ismene subg. *Elisena*	2–4	Peru and Ecuador at mid to high elevations	Present	Zygomorphic, large, white, not fragrant, 2–10, subsessile, declinate; tube short; staminal cup ± large, deflexed from the tube, free filaments long and declinate.	2	Absent	$2n = 46$
Ismene subg. *Pseudostenomesson*	2	Peru, above 3000 m	Present	Funnelform-tubular, actinomorphic, ± small, green, not fragrant, numerous, pedicellate, pendulous; tube long; staminal cup subcylindrical, free filament straight.	2	Absent	$2n = 46$
Hymenocallis	ca. 50	SE U.S., West Indies, Mesoamerica	Absent	Pancratioid, actinomorphic, large, white, fragrant, 1 to many, mostly sessile, erect; tube long; staminal cup large or small and variable in shape, not striped within; free filament long and straight.	2–10	Absent	$2n = 46$, 40 most common but variable

Table 2. Vouchers and new GenBank accession numbers for DNA sequences of Hymenocallideae. All vouchers are deposited at FTG unless otherwise indicated.

Taxon	Voucher	Origin	GenBank accession no. or previous citation		
			*trn*L gene	*trn*L-F spacer	ITS
Hymenocallis acutifolia (Herb.) Sweet	*Meerow 2424*	Mexico	—	—	Meerow et al. (2000a)
H. glauca M. Roem.	*Meerow 2433*	Mexico	—	—	Meerow et al. (2000a)
H. latifolia (Mill.) Roem.	*Meerow 2438*	Florida, USA	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)
H. eucharidifolia Bak.	*Meerow 2439*	Mexico	AF411078	AF411079	Meerow et al. (2000a)
H. tubiflora Salisb.	*Meerow 2440*	Trinidad	—	—	Meerow et al. (2000a)
Ismene subg. *Ismene*					
Ismene amancaes (Ruiz & Pav.) Herb.	*Meerow 2452*	Peru	—	—	AF411080
I. hawkesii (Vargas) Gereau & Meerow	*Meerow 2441*	Peru	—	—	Meerow et al. (2000a)
I. narcissiflora Jacq.	*Meerow 2306*	Peru	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)
Ismene subg. *Elisena* (Herb.) Meerow					
I. longipetala (Lindl.) Meerow	*Sagastegui 15454*	Peru	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)
Ismene subg. *Pseudostenomesson* (Velarde) Meerow					
I. vargasii (Velarde) Gereau & Meerow	*Meerow 2308*	Peru	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)
Leptochiton quitoensis (Herb.) Sealy	*Meerow 1116*	Ecuador	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)
Pamianthe peruviana Stapf	*Meerow 2304*	Peru	Meerow et al. (1999)	Meerow et al. (1999)	Meerow et al. (2000a)

Table 3. Characters and character states used in the cladistic analyses of Hymenocallideae based on morphology.

Character	States and coding
1. Elongate pseudostem	absent (0); present (1)
2. Flower number	2–10 (0); solitary (1); >10 (2)
3. Flowers sessile/pedicellate	sessile (0); pedicellate (1)
4. Flower habit	erect (0); declinate/horizontal (1); pendent (2)
5. Tube length	shorter than tepals (0); longer than or equal to tepals (1)
6. Tube habit	straight (0); curved (1)
7. Perianth morphology	pancratioid (0); funnelform-tubular (1); ± funnelform (2)
8. Perianth symmetry	actinomorphic (0); zygomorphic (1)
9. Flower color	white (0); yellow (1); green (2)
10. Fragrance	present (0); absent (1)
11. Staminal cup shape	rotate or funnelform (0); cylindrical (1)
12. Staminal cup striping	present (0); absent (1)
13. Free filament	incurved (0); straight (1); declinate (2)
14. Free filament	longer than cup (0); shorter than cup (1)
15. Pollen grain size	very large (0); large (1); medium (2)
16. Pollen grain	auriculate (0); not (1)
17. Exine reticulum	coarse (0); medium (1)
18. Ovules per locule	>20 (0); 16–20 (1); 2–10 (2); 2–4 (3)
19. Seed per locule	numerous (0); 2–5 (1); 1 (2)
20. Phytomelan on testa	present (0); absent (1)
21. Seed coat	not fleshy (0); fleshy (1)
22. Seed shape	flat, winged (0); globose (1)
23. Most common diploid chromosome number	46 (0); 34 (1); 46, 40 (2)

SEQUENCE ALIGNMENTS

Both sequence matrices were readily aligned manually using the program Sequencher (Gene-Codes, Inc., Ann Arbor, Michigan) as few gaps needed to be inserted.

CLADISTIC ANALYSES

Pamianthe (tribe Clinantheae) was used as outgroup for all analyses. In larger sequence analyses (Meerow et al., 1999, 2000a), this genus resolves as most closely related to the Hymenocallideae. *Pamianthe* and *Leptochiton* (the latter putatively the least derived genus in the Hymenocallideae; see discussion below) share two four-base sequence elements in the *trn*L-F region (bp325–328, 821–824) that are absent from the rest of the Hymenocallideae. Phylogenetic analyses were run using PAUP* version 4.0b8 beta (Swofford, 1998). An exhaustive search of all possible tree topologies was conducted

Table 4. Character state matrix for cladistic analysis of 23 morphological characters in Hymenocallideae. Polymorphisms: + = (0,1); * = (0,1,2).

Taxon	Matrix
	1 2
Character	12345678901234567890123
Hymenocallis acutifolia	00001000000110000221112
Hymenocallis eucharidifolia	0*001000000130000221112
Hymenocallis glauca	0*001000000130000221112
Hymenocallis latifolia	0*001000000130000221112
Hymenocallis tubiflora	0*001000000130000221112
Ismene amancaes	10111+00100001000321110
Ismene hawkesii	10111+00000001000321110
Ismene longipetala	10110021011120211321110
Ismene narcissiflora	10111+00000001000321110
Ismene vargasii	10120110211110211321110
Leptochiton quitoensis	01001100+00001000110111
Pamianthe peruviana	10111000000001110000000

for *trn*L-F. For ITS, the morphological, and all combined analyses, branch and bound searches were conducted. Support for internal nodes of the trees was determined with 5000 replicates of branch and bound bootstrapping (Felsenstein, 1985) and by calculation of Bremer (1988) decay indices (DI) using the program TreeRot (Sorenson, 1999). A branch and bound search was implemented for each constraint statement postulated by TreeRot. A bootstrap value of 50–64% was considered weak, 65–74% moderate, and 75–100% strong support.

Combining independent character matrices, whether both molecular or molecular and morphological, very often increases the resolution of the ingroup and the bootstrap support of the internal nodes of the phylogenetic trees (Olmstead & Sweere, 1994; Chase et al., 1995; Yukawa et al., 1996; Rudall et al., 1998; Soltis et al., 1998; Meerow et al., 1999). Nonetheless, there is controversy about whether different data sets should be analyzed separately or together (De Queiroz et al., 1995; Huelsenbeck et al., 1996). Congruence of the independent matrices has generally been demonstrated before they are combined, but it has also been argued that incongruence should not be a predetermined factor against doing so (Dubuisson et al., 1998; Seelanan et al., 1997). Miyamoto and Fitch (1995) argued that data sets should always be analyzed independently, as underlying assumptions, constraints, or weighting strategies will vary from data set to data set. Kluge (1989) and Nixon and Carpenter (1996) argued that simultaneous analysis of multiple data sets better maximizes parsimony and allows secondary signals to appear from the combined data. Bull et al. (1993), Rodrigo et al. (1993), and De Queiroz (1993) advocated combining data only after a statistical test of congruence, what Huelsenbeck et al. (1996) called "conditional combination." Before combining the data sets, we performed a partition homogeneity test (Farris et al., 1994, 1995) on the variously combined matrices, using a branch and bound search.

Results

Morphological matrix

With all characters unordered, two most parsimonious trees (Fig. 1A, one shown) were found of length = 37, consistency index (CI) = 0.86, and retention index (RI) = 0.88. Sixteen of the 23 characters used were parsimony informative. In both trees, *Hymenocallis* is monophyletic (bootstrap = 89%, DI = 1), while *Ismene* is paraphyletic. *Ismene longipetala* (subg. *Elisena*) and *I. vargasii* (subg. *Pseudostenomesson*) are sisters in both trees. *Leptochiton* is sister to both *Hymenocallis* and *Ismene* in one tree (Fig. 1A). The 6 apomorphies at the ancestral node are an increase in pollen grain size, auriculate pollen grains, reduction in ovule number from more than 20 to 16 to 20; reduction in number of seeds per locule; and evolution of globose, fleshy seeds. Apomorphies for *Hymenocallis* (Fig. 1A) are the absence of an elongate pseudostem, predominantly sessile and erect flowers, and $2n$ = 46, 40 chromosomes. Other than *Hymenocallis*, the only clade with strong bootstrap support is the sister relationship of *Ismene* subg. *Elisena* and subgenus *Pseudostenomesson* (100%, DI = 6), based on 7 apomorphies: perigone tube length reduction, non-pancratioid floral morphology, loss of floral fragrance, cylindrical staminal cup, and smaller non-auriculate pollen grains with less coarse exine reticulum. If all of the characters are ordered as irreversible, a single tree is found of length = 48, with CI = 0.67 and RI = 0.88 (Fig. 1B). There is moderate bootstrap support for a monophyletic *Ismene* (65%; DI = 2; apomorphies: elongate pseudostem, pedicellate and declinate/horizontal flowers, and 2–4 ovules per locule). There is weak support for the sister relationship of *Hymenocallis* and *Ismene* (56%, DI = 1; apomorphies: reduction in ovule and seed number, respectively; and the loss of phytomelan from the testa). *Leptochiton* is moderately supported as sister to both (65%, DI = 1; apomorphies: reduction in ovule and seed number and the evolution of a fleshy seed). *Ismene* subg. *Ismene* has a 91% bootstrap and DI = 2. *Ismene* subg. *Elisena* (*I. longipetala*) and subgenus *Pseudostenomesson* (*I. vargasii*) are again sister groups with 100% bootstrap and a DI = 9. A monophyletic *Hymenocallis* receives 87% bootstrap support with a DI = 4. *Hymenocallis latifolia*, *H. glauca*, and *H. eucharidifolia* form a monophyletic group with bootstrap support of 60 and DI = 1. This same tree topology (Fig. 1B) is 40 steps long with CI = 0.80 and RI = 0.80 if a branch and bound search is run with the topology as a constraint with all characters unordered.

Plastid *trn*L-F sequences

Using *trn*L-F sequences, which provide 7 parsimony-informative base substitutions, three equally most parsimonious trees are found of length = 82, CI = 0.99, and RI = 0.88 (Fig. 2, one tree shown). All three trees resolve a monophyletic *Ismene* with 81% bootstrap support (DI = 2), and *Leptochiton* as sister to the rest of the tribe but without support. A monophyletic *Hymenocallis* is resolved as sister to *Ismene* in one tree (Fig. 2), but *Hymenocallis* and

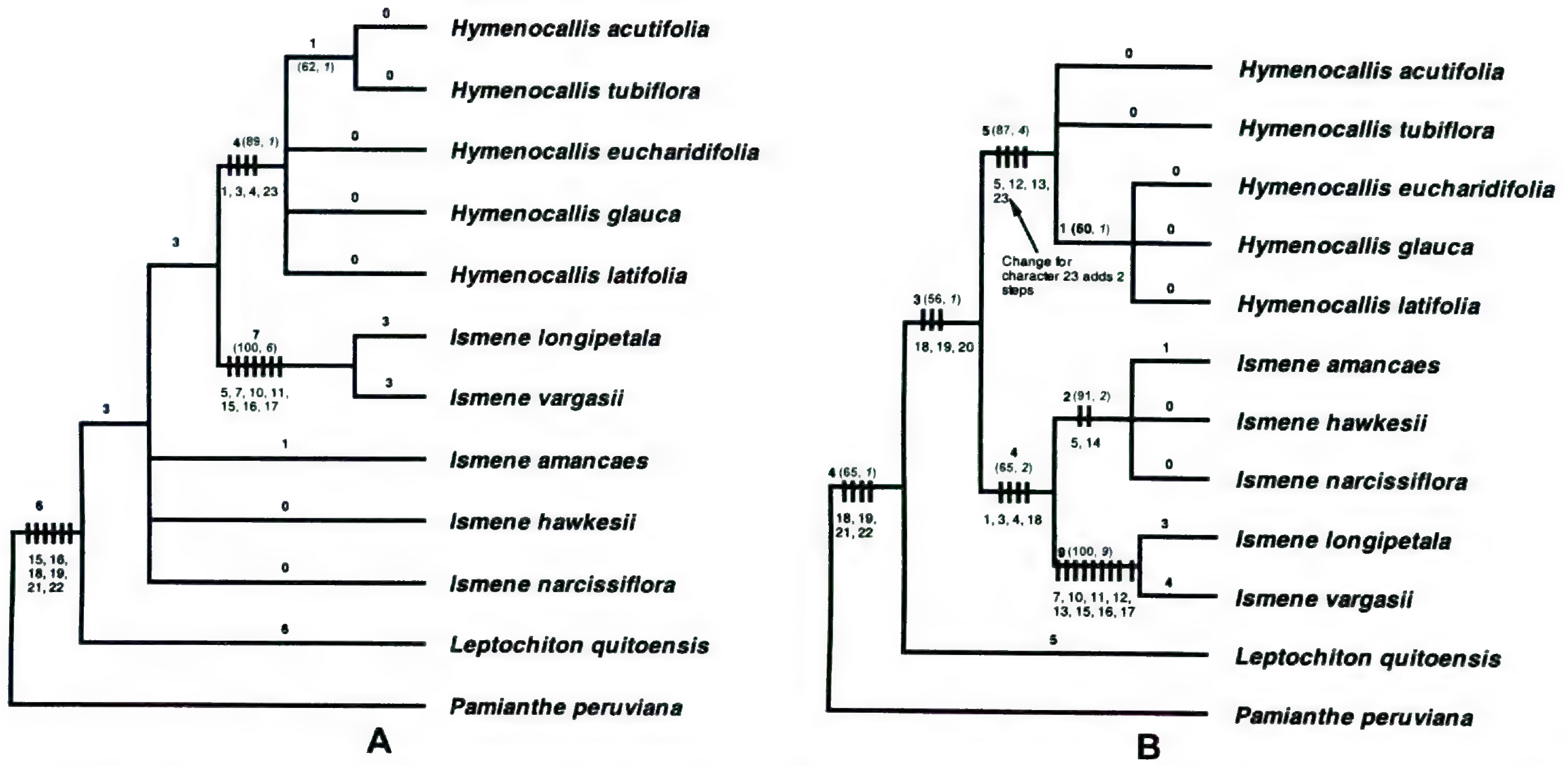


Figure 1. Cladograms for Hymenocallideae based on morphological characters. —A. One of two most parsimonious trees found with all characters unordered. —B. Single most parsimonious tree found if all characters are ordered as irreversible. Numbers above branches are branch lengths. Bootstrap percentages and decay indices (italic) are in parentheses. Vertical lines and numbers below branches are apomorphies along that branch (see Table 3).

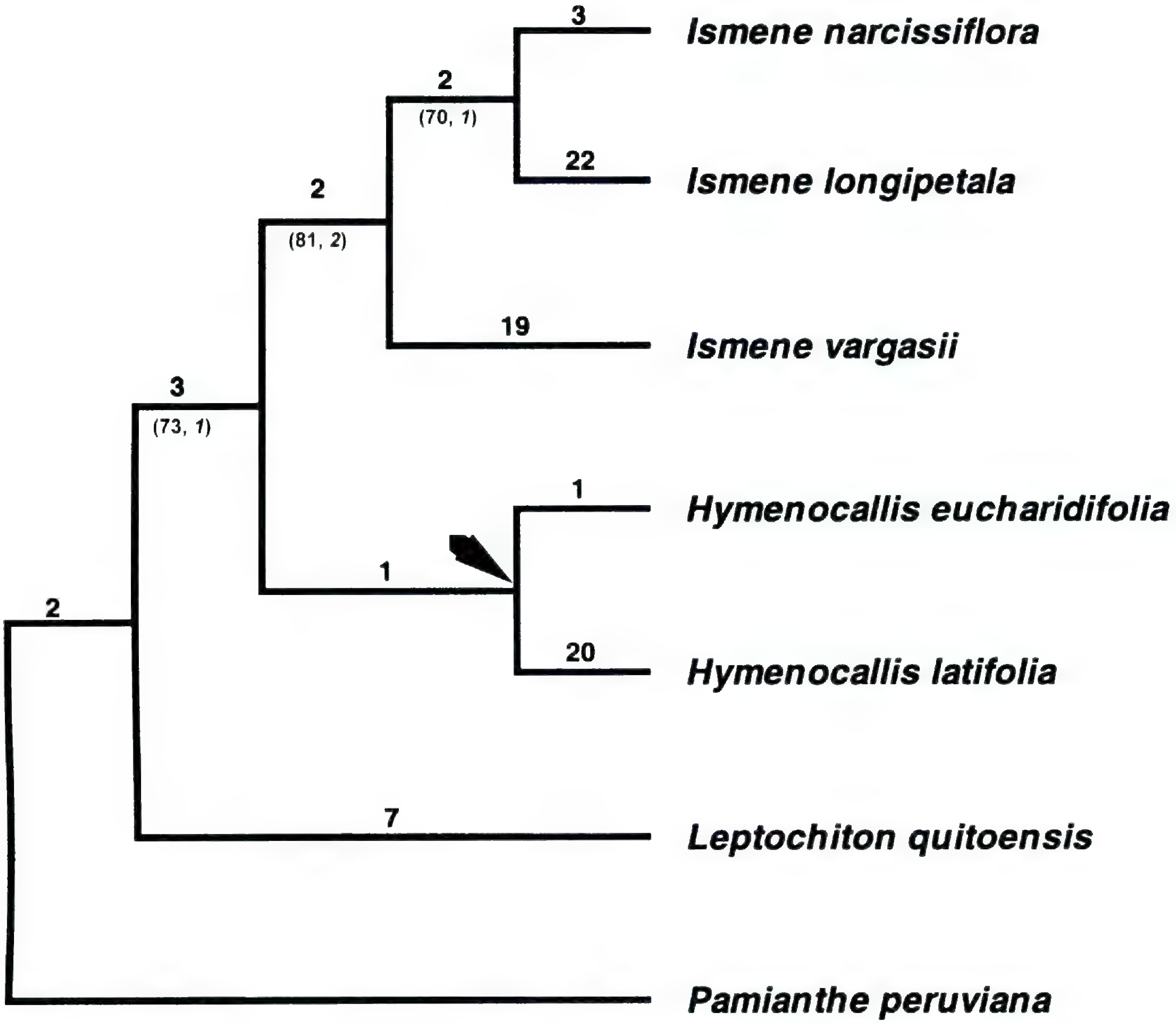


Figure 2. One of the three most parsimonious trees found by cladistic analysis of plastid *trn*L-F DNA sequences for the Hymenocallideae. Numbers above branches are branch lengths; numbers below branches are bootstrap percentages, followed by decay indices (italic). The large arrow indicates a node that collapses in the strict consensus of all three trees.

Ismene form a clade in all three (73% bootstrap, DI = 1). *Ismene* subg. *Ismene* (*I. narcissiflora*) and *Elisena* (*I. longipetala*) are resolved as sister groups in all three trees with a bootstrap of 70% (DI = 1).

ITS SEQUENCES

ITS provides 50 parsimony-informative characters, and 9 trees of length = 209, CI = 0.73, and RI = 0.77 were found (Fig. 3). In all of the trees, *Leptochiton* is resolved as sister to both *Hymenocallis* and *Ismene* (Fig. 3A), but without significant support. *Hymenocallis* is monophyletic (bootstrap = 97%, DI = 5), but *Ismene* is monophyletic in only 2 of the 9 trees (Fig. 3B, one shown). However, *Ismene* subg. *Ismene* (*I. amancaes*, *I. hawkesii*, *I. narcissiflora*) is monophyletic with weak bootstrap support (59%) and DI = 1 (Fig. 3B).

COMBINED *trn*L-F AND ITS SEQUENCES

The P value from the partition homogeneity test = 0.93, indicating that the *trn*L-F and ITS sequence matrices were highly congruent. Six most parsimonious trees were found of length = 292, CI = 0.92, and RI = 0.77 (Fig. 4). In all trees, *Hymenocallis* and *Ismene* are monophyletic sister genera with bootstrap support of 94% and a DI = 3. *Leptochiton* is sister to both, but without significant support. Bootstrap support for a monophyletic *Hymenocallis* is 98% (DI = 5), but only 68% (DI = 1) for a monophyletic *Ismene*. The only other internal resolution within *Ismene* that receives bootstrap support is a sister relationship between *I. narcissiflora* and *I. hawkesii* (both within subg. *Ismene*) at 84% with DI = 2.

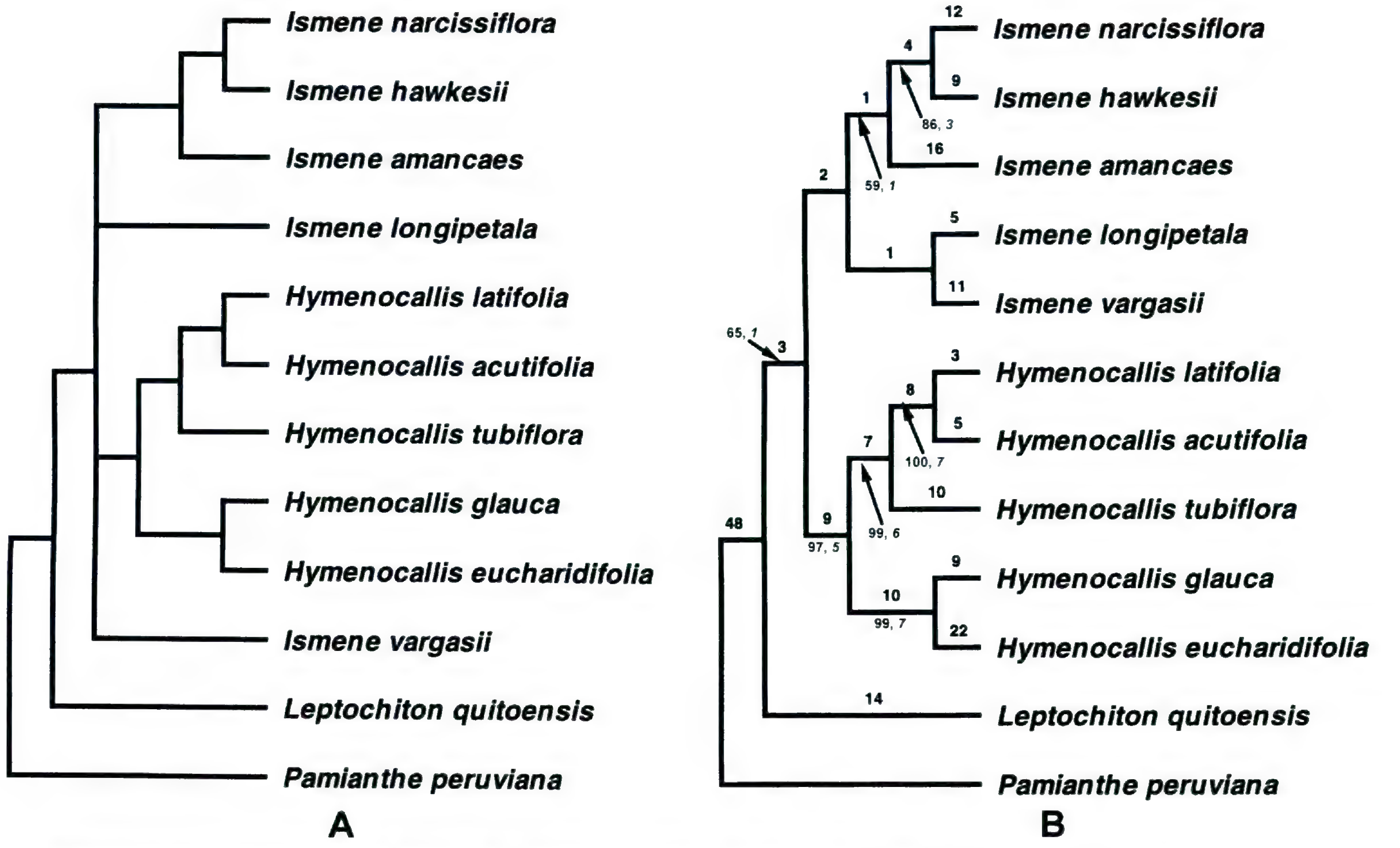


Figure 3. Cladograms for Hymenocallideae based on nrDNA ITS sequences. —A. Strict consensus of nine equally parsimonious trees. —B. One of two trees in which *Ismene* is a monophyletic sister group to *Hymenocallis*. Numbers above branches are branch lengths; numbers below branches are bootstrap percentages followed by decay indices (italic).

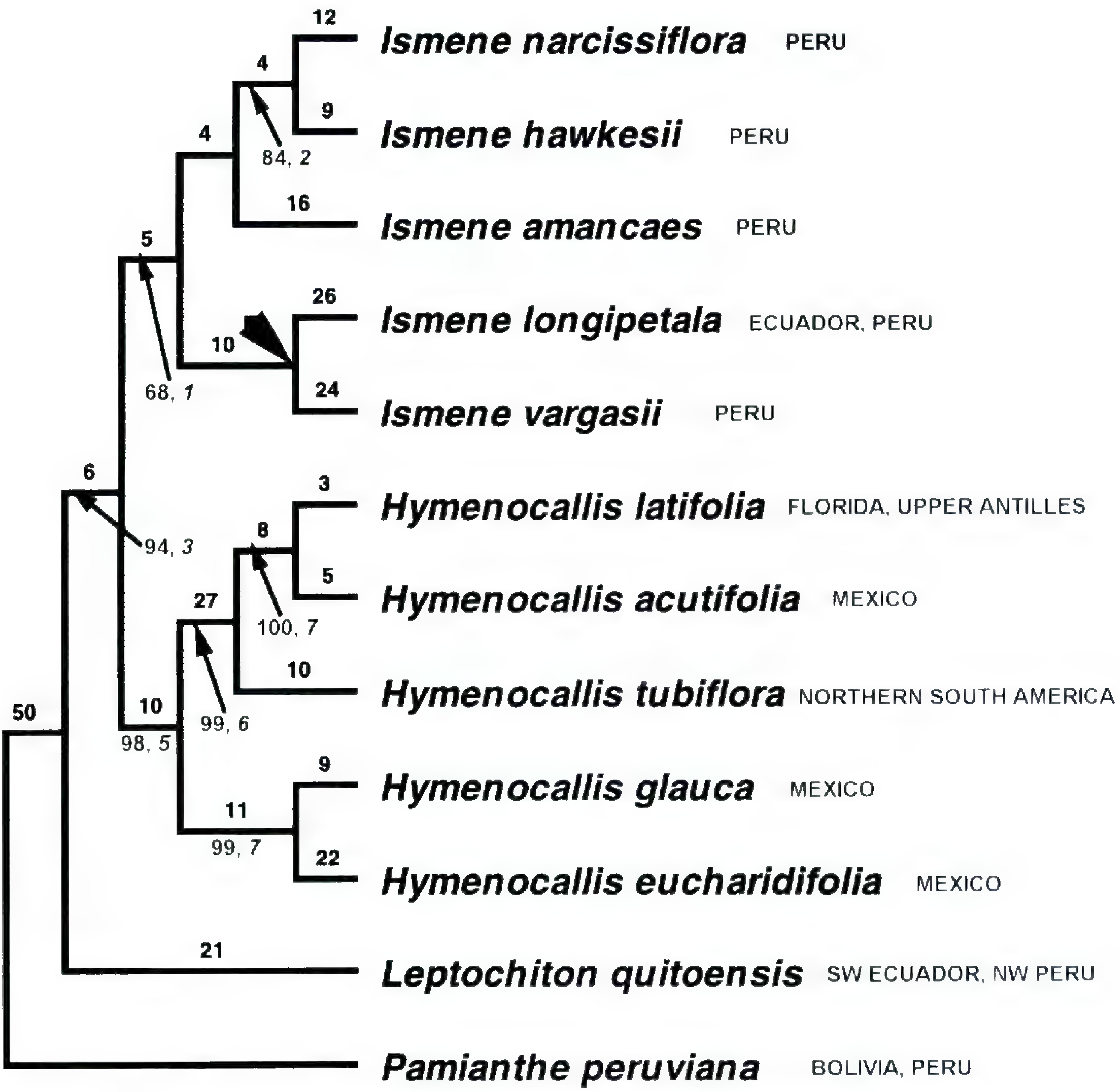
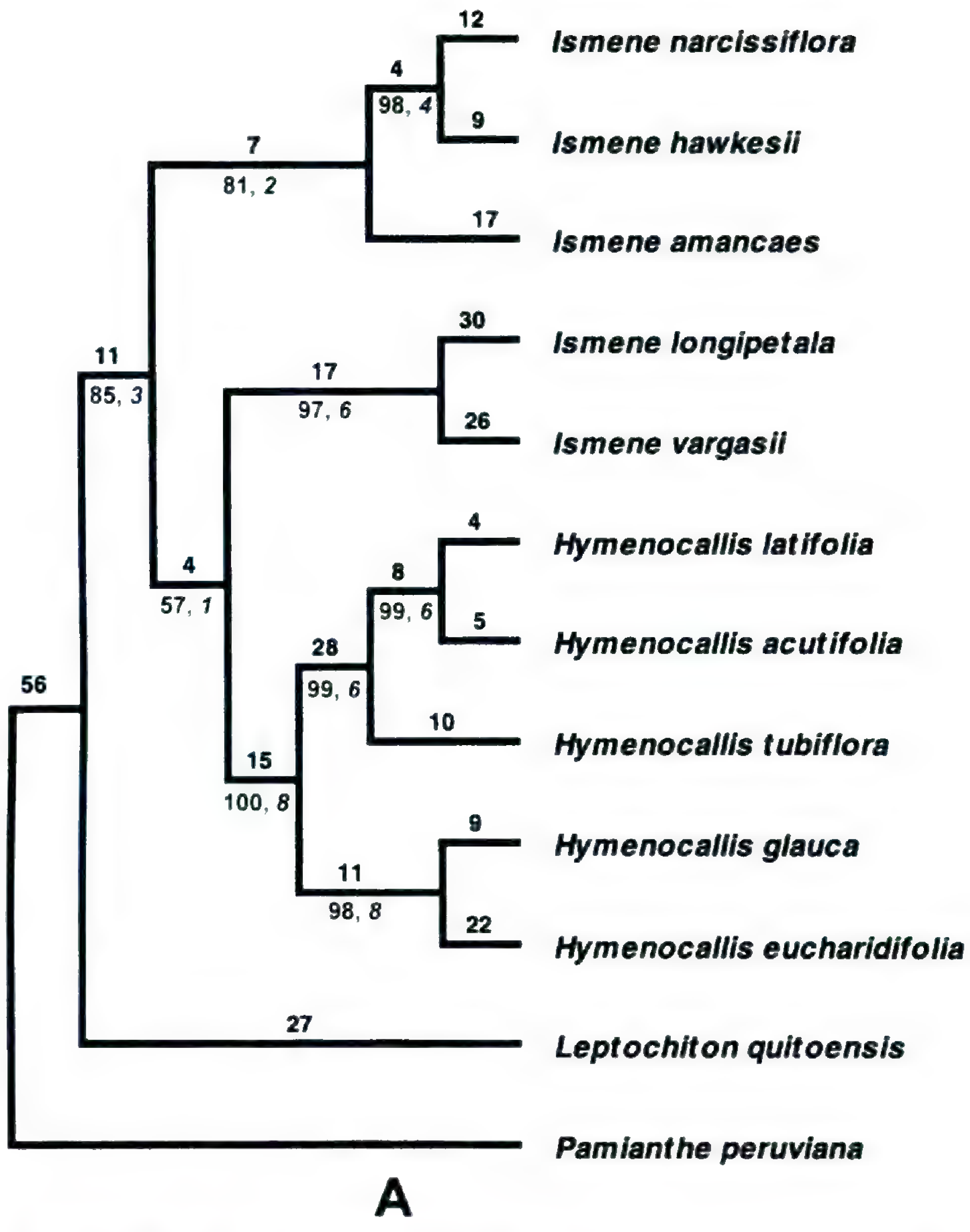


Figure 4. One of six most parsimonious trees found by cladistic analysis of combined plastid *trn*L-F and nrDNA ITS sequences. Numbers above branches are branch lengths; numbers below branches are bootstrap percentages followed by decay indices (italic). The larger arrow indicates a node that collapses in the strict consensus of all six trees.

COMBINED SEQUENCE AND MORPHOLOGICAL MATRICES

The P value of the partition homogeneity test was 0.0003, indicating significant incongruence between the morphological and DNA sequence data matrices. Much of the apparent incongruence can be attributed to the weak resolution of the morphologically based topologies, and we felt that it would still be informative to combine the two matrices in a single analysis. Of the 1565 characters included, 76 were parsimony informative. A single tree was found of length = 332, CI = 0.92, and RI = 0.79 (Fig. 5A). *Hymenocallis* is monophyletic with 100% bootstrap support (DI = 8), but *Ismene* is paraphyletic. Bootstrap support for the monophyly of *Ismene* subg. *Ismene* rises to 81% (DI = 2), but *Ismene* subg. *Elisena* (*I. longipetala*) and *Pseudostenomesson* (*I. vargasii*) are sister groups (bootstrap = 97%, DI = 4) weakly supported (bootstrap = 57%, DI = 1) as sister to *Hymenocallis*. *Leptochiton* is again sister to the other members of Hymenocallideae but without support. If trees one step longer were also retained in the search, in addition to the single shortest tree (Fig. 5A), a single, fully resolved tree of length = 333, CI = 0.90, and RI = 0.77 was found (Fig. 5B). In this tree (Fig. 5B), both *Hymenocallis* and *Ismene* are monophyletic sister genera, as are *Ismene* subg. *Elisena* and *Pseudostenomesson*.



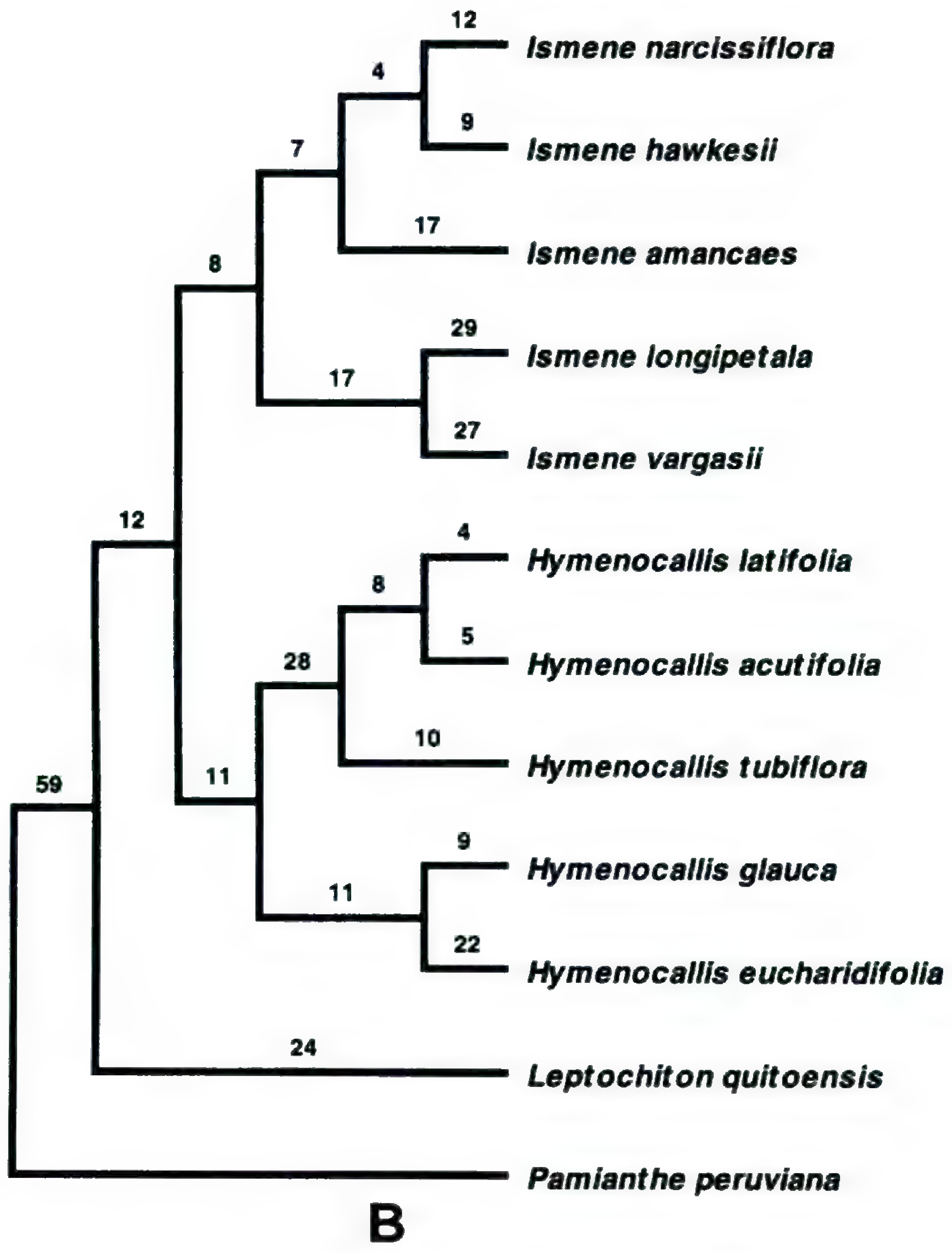


Figure 5. Cladograms for Hymenocallideae based on combined morphological and DNA sequence matrices. —A. Single most parsimonious tree. Numbers above branches are branch lengths; numbers below branches are bootstrap percentages followed by decay indices (italic). —B. Single additional tree found if trees one step longer than tree pictured in 5A are retained. Numbers above branches are branch lengths.

Discussion

Both plastid (Meerow et al., 1999) and ITS (Meerow et al., 2000a) sequences strongly support the position of the tribe Hymenocallideae as a monophyletic group within the Andean tetraploid clade of the endemic American Amaryllidaceae that is sister to the newly recognized tribe Clinantheae Meerow (Meerow et al., 2000a). The seeds of the Clinantheae are uniformly dry, flat, winged, and with phytomelanous testas. There are links between *Leptochiton* and *Pamianthe* that Stapf implicitly recognized, most notably the plesiomorphic presence of phytomelan in the testa of *Leptochiton*'s seed [of which Meerow & Dehgan (1985) were unaware], but also the numerous ovules of this genus (plesiomorphic as well). In the ITS phylogeny presented by Meerow et al. (2000a), support for *Pamianthe* as sister to the rest of Clinantheae (vs. a sister group relationship to Hymenocallideae or an unresolved position) was considerably weaker when the aligned matrix was not successively weighted. This is not surprising given that both genera occupy a basal phylogenetic position in their respective clades herein.

The difficulty of relying on morphological characters alone to generate phylogenies in Amaryllidaceae has been discussed (Meerow, 1995; Meerow et al., 2000b), given a high degree of homoplasy for many morphological characters in the family. Our analysis (Fig. 1) generates trees with relatively high CI and RI, but parsimony is still not able to resolve *Ismene* nor consistently place *Leptochiton* in the basal position within the tribe with unordered morphological characters alone, in contrast to sequence data (Figs. 2–4), which also provide (in the combined *trn*L-F and ITS matrix), over three times the number of phylogenetically informative characters of morphology alone. The combined plastid and nuclear sequence matrix produces the most fully resolved shortest trees. To "force" this topology upon any of the other conflicting data matrices requires either ordering characters or accepting longer trees (albeit only one step longer in the combined sequence and morphological analysis).

When biogeographic information is optimized upon the combined plastid and nrDNA tree (Fig. 4), the gene phylogeny supports an origin for the tribe in the central Andes, inarguably a locus of diversity for the Andean tetraploid clade of the Amaryllidaceae (Meerow et al., 2000a), with a vicariance event that gave rise to the largely North American *Hymenocallis*. *Leptochiton*, with 16 to 20 ovules per locule and a phytomelanous testa, occupies a relict position in the tribe with links to the non-fleshy seeded Andean endemic Clinantheae. However, it is the genus *Ismene* that reflects the patterns of floral morphological diversity that occur in the Eustephieae, Clinantheae, and Stenomesseae (sensu Meerow et al., 2000a). *Ismene* subg. *Ismene* retains the plesiomorphic pancratioid floral morphology of *Leptochiton*, *Pamianthe*, and *Hymenocallis*, while the smaller *Ismene* subg. *Elisena* and subg. *Pseudostenomesson* express floral novelties. *Ismene* subg. *Pseudostenomesson*, occurring at the highest elevations of any member of the tribe, might be the youngest element of the polymorphic *Ismene*, since the Andes likely did not extend above 1000 m elevation before the Pliocene (10 MYBP; Van der Hammen, 1974, 1979). Analogous patterns of floral diversity are found throughout the tetraploid Andean clade of the American Amaryllidaceae. In the Clinantheae, the low- to mid-elevation genera *Pamianthe* and *Paramongaia* Velarde have pancratioid floral morphology, while the mostly high-elevation *Clinanthus* Herb. has colorful, putatively ornithophilous flowers. In the more distantly related petiolate-leafed Stenomesseae, *Eucharis* has the pancratioid flower; *Plagiolirion* resembles a miniature *Ismene* subg. *Elisena*; and *Stenomesson* and *Urceolina* exhibit colorful, putatively ornithophilous flowers. Finally, in the Eustephieae, which is sister to rest of the Andean clade (Meerow et al., 2000a), the full range of variation is evident in a single genus, *Hieronymiella* Pax (Hunziker, 1969). This recurrent pattern suggests a scenario of rapid mosaic evolution (sensu Stebbins, 1984) within this monophyletic, tetraploid group (Meerow, 1987). The relatively low number of phylogenetically informative base substitutions in our sequence analyses of non-coding regions (7 for *trn*L-F; 50 for ITS) supports a hypothesis of a relatively recent radiation within the Hymenocallideae tied to the rise of the Andes. This seems most significant relative to *Ismene*, the most polymorphic of the three hymenocallid genera, and the only one that has adapted to high elevation.

Hymenocallis is most speciose in Mexico (Bauml, 1979), with a secondary area of diversity in the southeastern United States (Smith & Flory, 1990, 2001; Smith et al., 2001). Only three described species have been reported from South America: the broadly and coastally distributed *H. littoralis*, *H. pedalis*, and *H. tubiflora*. The genus does not occur at all in the Andes, and *H. tubiflora* is the only species of the three that is restricted to northern South America (including Trinidad-Tobago). The known distribution of the Hymenocallideae suggests two possible hypotheses, either a long-distance dispersal event from the Andean center of

origin, or extinction of intervening populations of a proto-*Hymenocallis* ancestor. The fleshy seed of *Hymenocallis* is the largest of all the endemic American Amaryllidaceae, exhibits no dormancy, and germinates within 3–4 weeks after release, whether or not in substrate (Whitehead & Brown, 1940; pers. obs.). The relatively heavy seed does not immediately seem amenable to long-distance dispersal, and no dispersal agent other than water has even been suggested for the genus. Thus ancestral extinction is a more convincing hypothesis, but without a better understanding of the historical biogeography of *Hymenocallis* and a well-resolved phylogeny of the genus a likely explanation for its distribution cannot be determined.

In summary, combined *trn*L-F and ITS sequences support the Meerow and Snijman (1998) treatment of Hymenocallideae with three genera: *Hymenocallis*, *Ismene*, and *Leptochiton*. *Leptochiton* is sister to the *Hymenocallis*/*Ismene* clade and retains two plesiomorphic characters of the Andean tetraploid clade: 16 to 20 ovules per locule and a phytomelanous seed coat. The central Andean endemism of *Ismene* and *Leptochiton* and the absence of *Hymenocallis* from this region further suggest a vicariance event at some point subsequent to the origin of the tribe. It is thus appropriate to formalize the recognition of the two new subgeneric combinations within *Ismene*.

Ismene subg. **Elisena** (Herbert) Meerow, comb. nov. Basionym: *Elisena* Herb., Amaryllidaceae, 75, 201. 1837. TYPE: *Ismene ringens* (Ruiz & Pav.) Gereau & Meerow, Novon 3: 29. 1993.

Ismene subg. **Pseudostenomesson** (Velarde) Meerow, comb nov. Basionym: *Pseudostenomesson* Velarde. Rev. Cienc. (Lima) 51: 47–51. 1949. TYPE: *Ismene vargasii* (Velarde) Gereau & Meerow, in L. Brako & J. Zarucchi, Monogr. Syst. Bot. Missouri Bot. Gard. 45: 1253. 1993.

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PHYLOGENETIC AND BIOGEOGRAPHIC DIVERSIFICATION IN *OSMORHIZA* (APIACEAE)[1]

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Abstract

Osmorhiza Raf. (Apiaceae) consists of 10 species disjunctly distributed in temperate Asia (1 sp.) and the Americas (9 spp.). *Osmorhiza berteroi* and *O. depauperata* show an American antitropical disjunction. Within North America, these two species are also disjunctly distributed in eastern and western North America and the Great Lakes regions. A phylogenetic analysis was conducted to clarify inter- and intraspecific relationships based on sequences of the ITS and 5.8S regions of nrDNA. With *Anthriscus*, *Geocaryum*, and *Myrrhis* as outgroups, the monophyly of *Osmorhiza* is strongly supported. The ITS phylogeny suggests the basal position of the Asiatic *O. aristata* and the monophyly of the nine New World species. The ITS sequence of *Osmorhiza aristata* is relatively divergent from those of all other species even though it is morphologically similar to the eastern North American *O. claytonii* and *O. longistylis* (which form a clade), suggesting early divergence followed by morphological stasis. *Osmorhiza berteroi*, *O. brachypoda*, *O. depauperata*, *O. mexicana*, *O. occidentalis*, and *O. purpurea* constitute a monophyletic group (= western North American clade). The morphologically distinct *O. glabrata* from the central Andes forms a trichotomy with the eastern North American clade (*O. claytonii* and *O. longistylis*) and the western North American clade in parsimony and maximum likelihood analyses. The 11 populations studied of the widespread *O. berteroi* form a clade, and showed little sequence divergence, suggesting recent establishment of the widely disjunct populations following long-distance dispersal. Disjunct populations of *O. depauperata* from the Rocky Mountains and eastern North America have an identical ITS profile. *Osmorhiza occidentalis*, however, shows a high level of infraspecific sequence divergence. The ITS phylogeny and the low sequence divergence values suggest rapid diversification of *Osmorhiza* in western North America.

Key words: Apiaceae, biogeography, disjunction, morphological stasis, *Osmorhiza*.

Osmorhiza Raf. (Apiaceae) comprises ten species, with one species in Asia, eight species in North America (three of which also occur in South America), and one species restricted to the central Andes. The distribution of species within the genus provides an ideal model for studying the evolution of both intra- and intercontinental disjunctions, with three distinct patterns represented among its members (Fig. 1; cf. also Lowry & Jones, 1984). According to the most recent classification of the genus (Lowry & Jones, 1984; see also Kartesz & Ghandi, 1993), the sole Asian species, *O. aristata*, is closely related to two species found in eastern North America (*O. claytonii* and *O. longistylis*). The second distributional pattern is seen in *O. berteroi* and *O. depauperata*, both of which exhibit an antitropical (often inappropriately referred to as "amphitropical," see Cox, 1990) disjunction between temperate North and South America. Also, the more distantly related *O. mexicana* subsp. *mexicana* has

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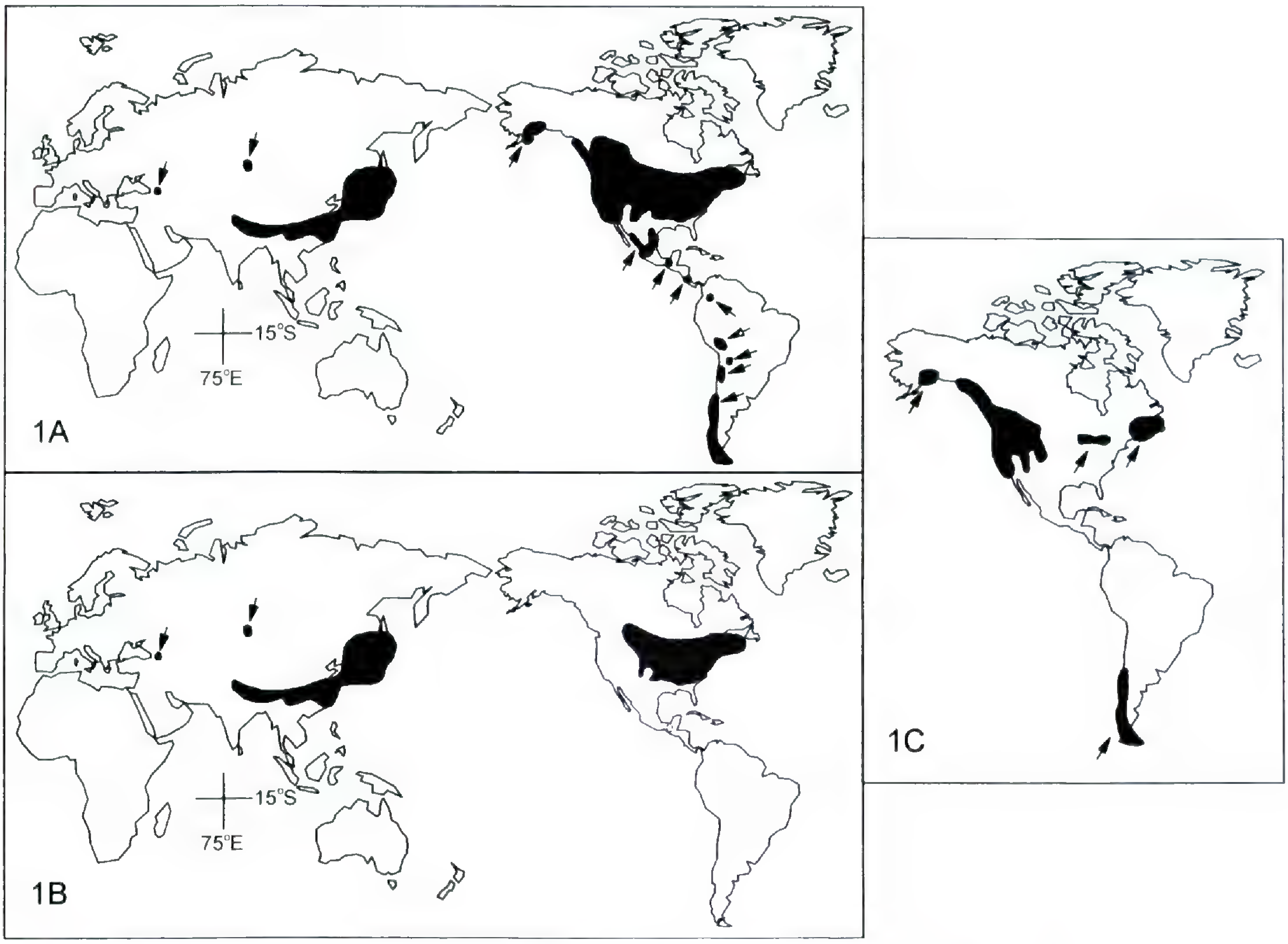

Figure 1.—A. Distribution of *Osmorhiza* (Apiaceae). —B. Distribution of *Osmorhiza* sect. *Osmorhiza*, showing Asian and eastern North American disjunction. —C. Distribution of *O. berteroi* showing American antitropical, and eastern–western North American disjunctions. Arrows indicate isolated areas of distributions.

a range that spans the American cordillera, with isolated populations extending from northern Mexico to northern Argentina. Finally, a third disjunction is found in *O. berteroi* and *O. depauperata*, in which populations occur in western North America, the Great Lakes region, and northeastern North America.

The disjunct distribution of plants between eastern Asia and eastern North America is a classic topic in biogeography (Gray, 1840, 1878; Li, 1952; Graham, 1972; Thorne, 1972; Boufford & Spongberg, 1983; Wu, 1983; Wen, 1998, 1999, 2001), and most genera exhibiting this pattern have now been well documented. Recent phylogenetic studies have confirmed the close affinity of the intercontinental disjuncts in many groups (reviewed in Wen, 1999), but most presumed species pairs studied so far between the two continents do not show a direct sister-species relationship. Morphological stasis (i.e., the lack of significant morphological change in a species over long periods of time) has been suggested as a common phenomenon among these disjuncts (Parks & Wendel, 1990; Qiu et al., 1995a, 1995b) and may at least partially explain the reported findings (Wen, 1999, 2001). To test this hypothesis, Wen (1998) suggested the examination of eastern Asian–eastern North American disjunct taxa within the context of biogeographic studies covering the Northern Hemisphere or even at a global scale. In-depth comparative studies of disjunct groups that also have apparent close relatives in western North America may provide insight into the relative morphological, molecular, physiological, and cladogenetic rates of evolution of taxa in all three areas.

Antitropical disjunctions between western North America and southern South America were recognized as early as 1880 by Gray and Hooker, and have been discussed by many authors since (e.g., Engler, 1882; DuReitz, 1940; Campbell, 1944; Constance, 1963; Raven, 1963; Cruden, 1966; Moore, 1972; Thorne, 1972, 1993; Cox, 1990; Peterson & Morrone, 1997; Peterson & Ortiz-Diaz, 1998). Constance (1963) pointed out that the species exhibiting this pattern comprise a highly unrepresentative sample of the floras in the two disjunct areas, and that many of them are self-compatible and often autogamous. Based on

these and other considerations, Raven (1963) concluded that the most plausible explanation for the observed antitropical disjunctions is relatively recent long-distance dispersal, although Cruden (1966) presented arguments in favor of "mountain hopping" that involves shorter distance dispersal along the western cordillera.

Fernald (1924, 1925, 1935) was the first to draw attention to disjunctions between western North America, the Great Lakes region, and northeastern North America, which he thought involved primarily arctic and western taxa that were able to survive during the Pleistocene in unglaciated areas ("nunataks") around Lake Superior, on the Gaspé Peninsula, and in Newfoundland and Labrador, but could not expand their range following the glaciations because of their antiquity. However, all of Fernald's nunataks were in fact glaciated, and the notion of senescent species is now widely rejected (Wood, 1972). A modified version of this hypothesis was proposed by Schofield (1969), who regarded the eastern populations as remnants of a previously widespread flora whose members were able to survive only in some areas (probably south of the glacial boundaries, but perhaps also in nunataks) and then move to their present sites following the Pleistocene, while being eliminated from the refugia. Lowry and Jones (1984) viewed this as a plausible explanation for the western North American–eastern North American disjunctions in *O. berteroi* and *O. depauperata*, and further suggested that taxa occurring in the Great Lakes area and the northeast are most likely now restricted to sites with less competition from eastern boreal taxa and where climatic conditions (especially snowfall and moisture availability in spring) are similar to those in western parts of the continent.

Another fascinating aspect of *Osmorhiza* is that the type of seed dormancy differs among the species, and in particular between the putative close relatives in eastern Asia and eastern North America. Very little comparative research has been done on physiological traits of species that exhibit this classical disjunct pattern (Terui & Okagami, 1993; Wen et al., 1996), with only one investigation conducted within a phylogenetic framework (Wen et al., 1996). Studies on seeds of five *Osmorhiza* species found that they have morphophysiological dormancy (MPD) (Baskin & Baskin, 1984, 1991; Baskin et al., 1995; Walck et al., 2002). Seeds with MPD have embryos that are very small relative to the size of the seed, and the embryo must grow to the full length of the seed to germinate. In addition to being small, the embryos also have physiological dormancy that must be broken before seeds can germinate (Baskin & Baskin, 1998). Seeds of *O. claytonii* and *O. longistylis* have nondeep complex MPD, i.e., they require warm followed by cold stratification to germinate, and gibberellic acid (GA_3) substitutes for warm stratification (Baskin & Baskin, 1984, 1991). In contrast, seeds of *O. aristata* and those from western North American populations of *O. berteroi* and *O. occidentalis* have deep complex MPD, requiring only cold stratification to overcome dormancy, and GA_3 does not substitute for stratification (Baskin et al., 1995; Walck et al., 2002). Thus, mapping the types of MPD on a phylogenetic tree can provide an opportunity to evaluate the evolution and adaptive significance of this physiological trait.

Constance and Shan (1948) proposed an infrageneric classification for *Osmorhiza* that was largely adopted by Lowry and Jones (1984) with a few modifications (Table 1). Several hypotheses of relationships are implied in this classification. Two subgenera are recognized, one of which (subg. *Glycosma*) comprises a single western North American species, *O. occidentalis*, which would thus represent the sister species to a clade that includes the remaining nine species. Within the typical subgenus, three sections are defined (each with three species), which are likewise assumed to comprise monophyletic groups. This classification thus offers a framework against which to test alternative hypotheses of relationships using molecular sequence data that were not available previously.

The objectives of this study are to: (1) reconstruct the phylogeny of *Osmorhiza* using sequences of the internal transcribed spacer (ITS) and 5.8S regions of nuclear ribosomal DNA; (2) examine the biogeographic diversification within the group; (3) re-evaluate the earlier hypotheses regarding the possible origins of the observed disjunct distributional patterns; and (4) examine the evolution of seed dormancy in a phylogenetic framework for disjunct taxa of *Osmorhiza* and determine which type(s) of MPD are plesiomorphic versus derived. Sequences of ITS and 5.8S regions were employed because they have been shown to be appropriate to assess evolutionary relationships within other groups exhibiting disjunct distributions between Asia and North America (Fritsch, 1996; Lee et al., 1996; Wen & Zimmer, 1996; Wen et al., 1998) as well as interspecific relationships in Apiaceae (Downie et al., 1998) and evolution within many other north temperate plants (e.g., Xiang et al., 1998; Lee & Wen, 2001).

Materials and Methods

Forty-eight populations representing all ten species of *Osmorhiza* and three outgroup taxa were

Table 1. Taxa of *Osmorhiza* Raf. and their distributions following the classification scheme of Lowry and Jones (1984), as modified from Constance and Shan (1948).

Classification	Taxon	Distribution
Subgenus *Glycosma* (Nutt.) Drude	*O. occidentalis* (Nutt.) Torr.	W North America
Subgenus *Osmorhiza*		
Section *Mexicanae* Constance & Shan ex Lowry & A. G. Jones	*O. brachypoda* Torr.	California, Nevada, and Arizona
	O. glabrata Phil.	central Andes
	O. mexicana Griseb.	
	subsp. *bipatriata* (Constance & Shan) Lowry & A. G. Jones	SW Texas and N Mexico
	subsp. *mexicana*	N Mexico to N Argentina
Section *Nudae* Constance & Shan ex Lowry & A. G. Jones	*O. berteroi* DC.	W North America, Great Lakes area, NE North America, and South America
	O. depauperata Phil.	W North America, Great Lakes area, NE North America, and South America
	O. purpurea (J. M Coult. & Rose) Suksd.	NW North America
Section *Osmorhiza*	*O. aristata* (Thunb.) Rydb.	temperate Asia
	O. claytonii (Michx.) C. B. Clarke	E North America
	O. longistylis (Torr.) DC.	E North America

sampled in this study (Table 2). Populations of widespread disjunct taxa such as *O. berteroi* and *O. depauperata* were examined from throughout much of their distributional ranges. *Anthriscus caucalis* M. Bieb., *Geocaryum macrocarpum* (Boiss. & Spruner) Engstrand, and *Myrrhis odorata* (L.) Scop. were chosen as the outgroups because of their close relationship to *Osmorhiza* (Lowry & Jones, 1984; Downie et al., 2000).

Total DNA was extracted with the CTAB method of Doyle and Doyle (1987) and purified over CsCl/ethidium bromide gradients. DNA amplifications were performed in 100-μL reactions following Wen and Zimmer (1996) using the primers C26A and Nnc18S10 (see Wen & Zimmer for sequences of primers). The entire ITS and 5.8S regions were sequenced manually from both directions following Wen et al. (1998) using four primers: C5.8S, C26A, ITS4, and N18L18 (see Wen & Zimmer for sequences of primers).

The DNA sequences obtained were assembled, and the boundaries between the coding and spacer regions were determined by comparing them with the sequences of *Daucus carota* L. (Yokota et al., 1989). The sequences were then exported to PAUP* (vers. 4.0, Swofford, 1999). Most mutations were base substitutions, thus allowing manual alignment. All the sequences have been deposited at GenBank (see Table 2 for accession numbers).

Phylogenetic analyses were performed with PAUP* using maximum parsimony (Swofford et al., 1996), maximum likelihood (Felsenstein, 1981), and neighbor-joining (Saitou & Nei, 1987) methods. Parsimony analysis was performed using a branch-and-bound search with MULPARS and furthest addition sequence options. The amount of support for monophyletic groups revealed in the maximally parsimonious tree(s) (MPTs) was examined with 1000 bootstrap replicates (Felsenstein, 1985) with random addition and heuristic search options. The maximum likelihood analysis was performed with the input order of sequences randomized and the transition/transversion ratio set at 1.42 based on the observed frequencies in the MPTs of the parsimony analysis. A neighbor-joining tree was constructed using Kimura two-parameter distance (Kimura, 1980).

Relative rate tests were performed with the method of Wu and Li (1985) to detect any rate asymmetries of the ITS and 5.8S regions among taxa in *Osmorhiza*. The proportions of site differences were estimated using the Kimura two-parameter distance (Kimura, 1980).

The optimal area cladogram was constructed from taxon cladograms using the optimality method in COMPONENT (vers. 2.0, Page, 1993). The following options were used: nearest-neighbor interchanges and minimizing the number of leaves added. Four areas of endemism were defined for *Osmorhiza* based on the distribution of taxa and previous biogeographic studies of the North Temperate zone (e.g., Wood, 1970; Patterson, 1981;

Table 2. Accessions of *Osmorhiza* species and the outgroup sampled. Collections marked with "*" were used in the relative rate tests (see Table 3).

Taxon	Voucher	Source	GenBank accession
O. aristata	*S. Zhou s.n. (F)	China, Zhejiang Prov.	AF453952
	K. Yonekura s.n. (F)	Japan, Aomori Pref.	AF453953
	J. H. Lee & B. W. Han s.n. (F)	Korea, Odaesan	AF453954
O. berteroi	*M. Baeza & G. Kottirsch 675 (F)	Chile, Prov. Ñuble	AF453955
	M. Baeza & G. Kottirsch 676 (F)	Chile, Prov. Ñuble	AF453956
	T. Stuessy et al. 15556 (F)	Chile, Valle Hermoso	AF453965
	M. Baeza & G. Kottirsch 1172 (F)	Chile, Prov. Malleco	AF453957
	L. P. Janeway & D. Isle 5710 (CS)	U.S.A., California, Colusa Co.	AF453963
	V. H. Oswald 9248 (CS)	U.S.A., California, Butte Co.	AF453964
	J. Wen 4707 (F)	U.S.A., Michigan, Luce Co.	AF453958
	J. Wen 4726 (F)	Canada, Quebec, Rimouski Co.	AF453959
	J. Wen 4732 (F)	Canada, Quebec, Gaspé Co.	AF453960
	P. P. Lowry II et al. 4949 (MO)	U.S.A., Oregon, Clackamas Co.	AF453961
	P. P. Lowry II et al. 4950 (MO)	U.S.A., Oregon, Marion Co.	AF453962
O. brachypoda	V. H. Oswald 9253 (CS)	U.S.A., California, Butte Co.	AF453966
O. claytonii	*J. Wen 1069 (A)	U.S.A., Kentucky, Menifee Co.	AF453970
	J. Wen 1089 (A)	U.S.A., Pennsylvania, Blair Co.	AF453971
	J. Wen 4716 (F)	U.S.A., Michigan, Baraga Co.	AF453972
	J. Wen 812 (A)	U.S.A., Maryland, Baltimore Co.	AF453969
	J. L. Walck & S. N. Hidayati 565 (F)	U.S.A., Kentucky, Fayette Co.	AF453967
	J. L. Walck & S. N. Hidayati 567 (F)	U.S.A., West Virginia, Pocahontas Co.	AF453968
O. depauperata	*J. Wen 3516 (F)	U.S.A., Colorado, Larimer Co.	AF453974
	J. Wen 4742 (F)	Canada, Quebec, Rimouski Co.	AF453975
	M. DeVore 1118 (OS)	Chile, Icalma Valley	AF453973
O. glabrata	*M. DeVore 1219 (OS)	Chile, Prov. de Talca	AF453976
	S. Teillier et al. 2419 (MO)	Chile, Frente a Santiago, PN El Morado	AF453977
O. longistylis	J. Wen 827 (A)	U.S.A., Virginia, Giles Co.	AF453979
	J. Wen 861 (A)	U.S.A., North Carolina, Watauga Co.	AF453980
	J. Wen 4715 (F)	U.S.A., Michigan, Baraga Co.	AF453981
	J. L. Walck & S. N. Hidayati 564 (F)	U.S.A., Kentucky, Fayette Co.	AF453978
O. mexicana subsp. *mexicana*	*H. Vibrans s.n. (10-VII-98) (CS)	Mexico, Edo	AF453983
	F. Chiang 1276 (CS)	Mexico, Mexico D.F.	AF453982
O. mexicana subsp. *bipatriata*	P. P. Lowry II & M. J. Warnock 3182 (F)	Mexico, Nuevo León	AF453984

Table 2. Continued.

Taxon	Voucher	Source	GenBank accession
O. occidentalis	**B. Painter et al. 18* (CS)	U.S.A., Colorado, Garfield Co.	AF453985
	J. Wen 3860 (F)	U.S.A., Colorado, Routt Co.	AF453986
	L. M. Moore 6672 (CS)	U.S.A., Colorado, Dolores Co.	AF453991
	V. H. Oswald & L. Ahart 9493 (CS)	U.S.A., California, Plumas Co.	AF453992
	V. H. Oswald & L. Ahart 9532 (CS)	U.S.A., California, Nevada Co.	AF453993
	P. P. Lowry II 4633 (MO)	U.S.A., Nevada, Elko Co.	AF453987
	P. P. Lowry II 5155 (MO)	U.S.A., Nevada, Lander Co.	AF453988
	R. R. Halse 5561 (CS)	U.S.A., Oregon, Benton Co.	AF453989
	R. R. Halse 5565 (CS)	U.S.A., Oregon, Benton Co.	AF453990
O. purpurea	*P. P. Lowry II 4963* (MO)	U.S.A., Oregon, Tillamook Co.	AF453994
	P. P. Lowry II 5069 (MO)	U.S.A., Oregon, Linn Co.	AF453995
	P. P. Lowry II 5070 (MO)	U.S.A., Oregon, Linn Co.	AF453996
Anthriscus caucalis		Downie et al. (1998)	U79601, U79602
Geocaryum macrocarpum		Downie et al. (2000)	AF073605, AF073606
Myrrhis odorata		Valiejo-Roman et al. (1998)	AF077901

Hoey & Parks, 1991), work on *Osmorhiza* (Lowry & Jones, 1984), and results of this phylogenetic analysis. These areas are western North America, eastern North America, central Andes, and Asia. South America was not chosen as one of the areas of endemism because it is linked to western North America via disjunction and shares the same species, suggesting that it was recently colonized (also see Discussion).

Results

Characteristics of ITS Sequences

The combined length of the ITS1, 5.8S, and ITS2 regions in *Osmorhiza* species is 605 bases, with an ITS1 of 217–220 bases, a 5.8S of 164 bases, and an ITS2 of 224–225 bases. Two insertions in ITS1 were required to align the sequences within the genus. One occurs in the three accessions of Asian *O. aristata* (1 bp), and the other is a 3-bp insertion in *O. mexicana* subsp. *bipatriata*. Two additional insertions are in ITS2, each 1-bp in length. The alignment of sequences of *Osmorhiza* with those of the outgroup species required five additional 1-bp and one 2-bp indels, and sequences of *Osmorhiza* and the outgroups could be aligned manually without difficulty. The sequence divergence of *Osmorhiza* taxa and the outgroups ranges from 4.679 (between *Myrrhis odorata* and *O. berteroi*) to 14.05% (between *Anthriscus caucalis* and *O. mexicana* subsp. *mexicana*).

Phylogenetic Analyses

Of the 693 aligned positions, 116 sites were variable; of these, 62 were phylogenetically informative. Treating gaps as new characters, the parsimony analysis generated a single most parsimonious tree (MPT) with a total length of 157 steps, a consistency index (CI) of 0.860 (0.763 excluding uninformative characters), a retention index (RI) of 0.912, and a rescaled consistency index (RC) of 0.785 (Fig. 2). Treating gaps as missing data, the parsimony analysis produced a single MPT with an identical topology to Figure 2 with a length of 141 steps, a CI = 0.851 (0.756 when uninformative characters are excluded), an RI = 0.974, and an RC = 0.916. The tree from the weighted parsimony analysis (weighting transversions over transitions 1.42 times) also had an identical topology to the MPT shown in Figure 2. Several relationships are suggested by the parsimony analyses: (1) the three populations of *O. aristata* from Asia form a monophyletic group; (2) *O. clay-*

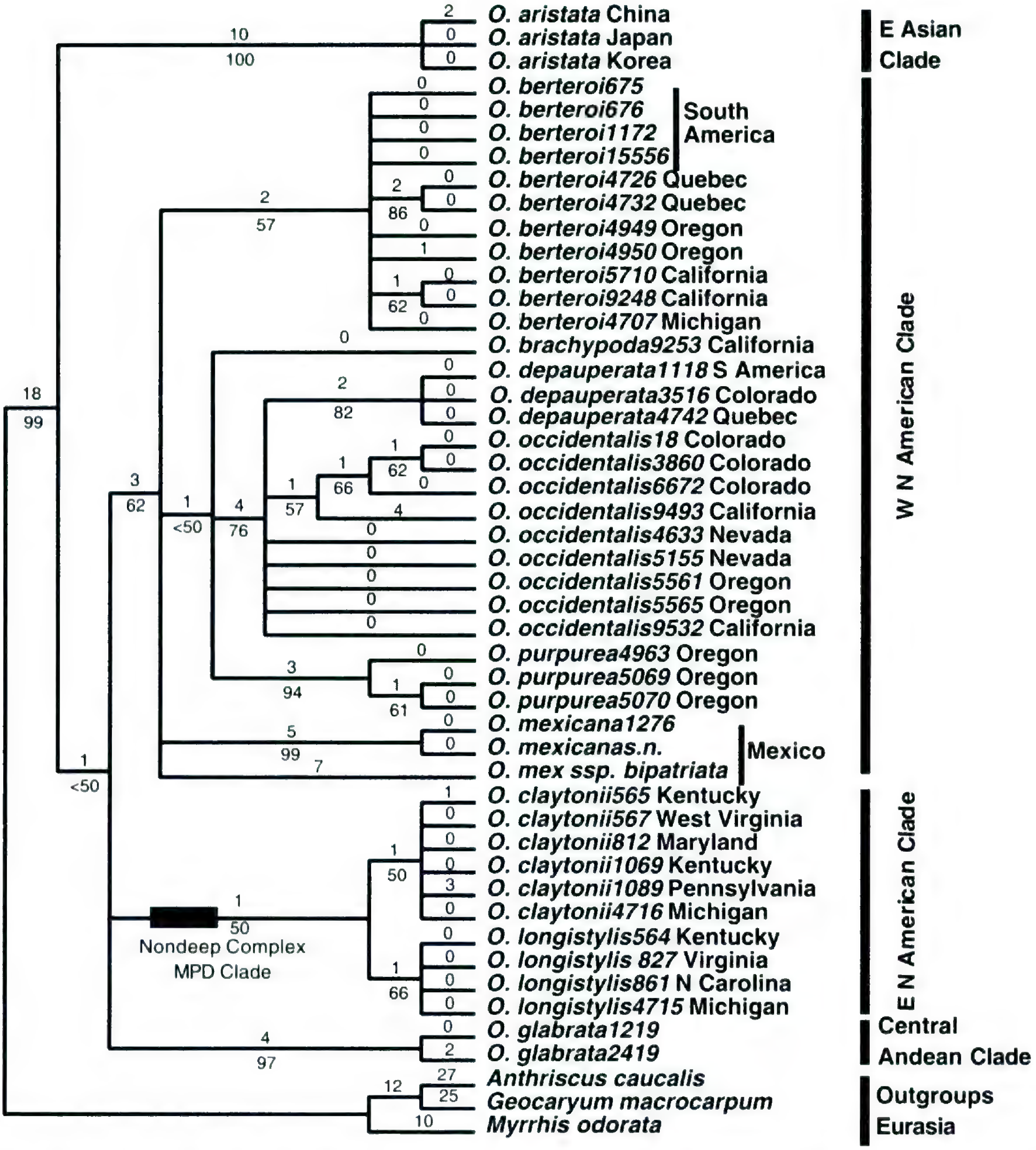

Figure 2. The single most parsimonious tree of *Osmorhiza* with a total length of 157 steps, a CI of 0.860 (0.763 excluding uninformative characters), an RI of 0.912, and an RC of 0.785, treating gaps as new characters. Numbers above lines are branch lengths and those below are bootstrap values in 1000 replicates. Numbers following the taxon names are accession numbers as in Table 2 to help identify the source of study material. The solid black bar at the node of the *O. claytonii–O. longistylis* clade indicates the most parsimonious explanation of the evolution of the nondeep complex morphophysiological dormancy (MPD).

tonii and *O. longistylis* from eastern North America form a clade (the E N American clade); (3) the multiple populations examined of the widespread *O. depauperata* form a monophyletic group; (4) *O. depauperata* and *O. occidentalis* form a clade; (5) *O. brachypoda* and *O. purpurea* are allied with the *O. depauperata–O. occidentalis* clade; (6) populations of the widespread *O. berteroi* form a monophyletic group; (7) several species (*O. berteroi, O. brachypoda, O. depauperata, O. mexicana, O. occidentalis,* and *O. purpurea*) form a largely western North American clade with *O. berteroi* and *O. depauperata* extending to eastern North America and South America, and *O. mexicana* ranging from Texas to South America (the W N American clade); and (8) *O. glabrata* from the central Andes forms

Table 3. Relative rate tests to detect rate asymmetry. *Myrrhis odorata* was used as the reference taxon. (* Significant at the 5% level.)

Species 1	Species 2	K_{13}	K_{23}	$K_{13}–K_{23}$ ± SE
O. aristata	*O. berteroi*	0.06582	0.05165	0.01417 ± 0.00611*
O. aristata	*O. claytonii*	0.06582	0.06015	0.00567 ± 0.00619
O. aristata	*O. depauperata*	0.06582	0.06759	−0.00177 ± 0.00701
O. aristata	*O. glabrata*	0.06582	0.05347	0.01235 ± 0.00545*
O. aristata	*O. mexicana*	0.06582	0.06442	0.00140 ± 0.00669
O. aristata	*O. occidentalis*	0.06582	0.06993	−0.00411 ± 0.00752
O. berteroi	*O. claytonii*	0.05165	0.06015	−0.00850 ± 0.00499
O. berteroi	*O. depauperata*	0.05165	0.06759	−0.01594 ± 0.00450*
O. berteroi	*O. glabrata*	0.05165	0.05347	−0.00182 ± 0.00397
O. berteroi	*O. mexicana*	0.05165	0.06442	−0.01277 ± 0.00398*
O. berteroi	*O. occidentalis*	0.05165	0.06993	−0.01828 ± 0.00493*
O. claytonii	*O. depauperata*	0.06015	0.06759	−0.00744 ± 0.00619
O. claytonii	*O. glabrata*	0.06015	0.05347	0.00668 ± 0.00415
O. claytonii	*O. mexicana*	0.06015	0.06442	−0.00427 ± 0.00574
O. claytonii	*O. occidentalis*	0.06015	0.06993	−0.00978 ± 0.00641
O. depauperata	*O. glabrata*	0.06759	0.05347	0.01412 ± 0.00520*
O. depauperata	*O. mexicana*	0.06759	0.06442	0.00317 ± 0.00481
O. depauperata	*O. occidentalis*	0.06759	0.06993	−0.00234 ± 0.00347
O. glabrata	*O. mexicana*	0.05347	0.06442	−0.01095 ± 0.00477*
O. glabrata	*O. occidentalis*	0.05347	0.06993	−0.01646 ± 0.00550*
O. mexicana	*O. occidentalis*	0.06442	0.06993	−0.00551 ± 0.00568

a trichotomy with the E N American clade and the W N American clade.

The maximum likelihood tree (MLT, not shown, with a log likelihood of −1512.26) has an identical topology to the MPT. The neighbor-joining tree (NJT) is similar to the MPT and the MLT, but differs in that (1) *O. glabrata* is placed sister to the *O. claytonii–O. longistylis* clade in the NJT; and (2) the *O. claytonii–O. longistylis–O. glabrata* clade is sister to the Asian *O. aristata*. The new clades are weakly supported with bootstrap values less than 50%.

SEQUENCE DIVERGENCE

Treating gaps as missing data, the Kimura two-parameter distance among species of *Osmorhiza* was estimated to be 0.299–3.784%. These divergence values are comparable to those in *Aralia* sect. *Aralia*, which shows a similar disjunct pattern of distribution, with representatives in eastern Asia and in eastern and western North America (Wen et al., 1998). The highest divergence occurs between *O. occidentalis* from western North America and *O. aristata* from eastern China, and the lowest between *O. claytonii* and *O. longistylis* from eastern North America, which are sympatric throughout much of their ranges. Overall, divergence values between *O. aristata* and other members of the genus are comparatively high, ranging from 1.627% (with *O. claytonii*) to 3.784% (with *O. occidentalis*). Among the New World species, sequence divergence of *O. glabrata* from the central Andes ranges from 0.601% (with *O. longistylis*) to 2.552% (with *O. occidentalis*). The western North American *O. occidentalis* has a relatively high level of sequence divergence, ranging from 0.319% (with *O. depauperata*) to 2.552% (with *O. glabrata*). Infraspecific variation was detected in six species for which multiple samples were available, *O. aristata* (0–0.302%), *O. berteroi* (0–0.473%), *O. claytonii* (0–0.517%), *O. mexicana* (0–1.415%), *O. occidentalis* (0–1.013%), and *O. purpurea* (0–0.148%), whereas multiple populations sampled of *O. depauperata* and *O. longistylis* showed no variation in their ITS profiles, despite the fact that these species have wide distributions. The absence or relatively low level of sequence variation within these taxa supports the species level circumscriptions proposed by Lowry and Jones (1984). On the other hand, infraspecific variation within *O. occidentalis* was 1.013% between populations from the Rocky Mountains and those from California.

RELATIVE RATE TESTS

Twenty-one relative rate tests (Wu & Li, 1985) were conducted to detect rate asymmetry (Table 3). *Myrrhis odorata* was used as the reference taxon. Rate differences of most pairs of species were not

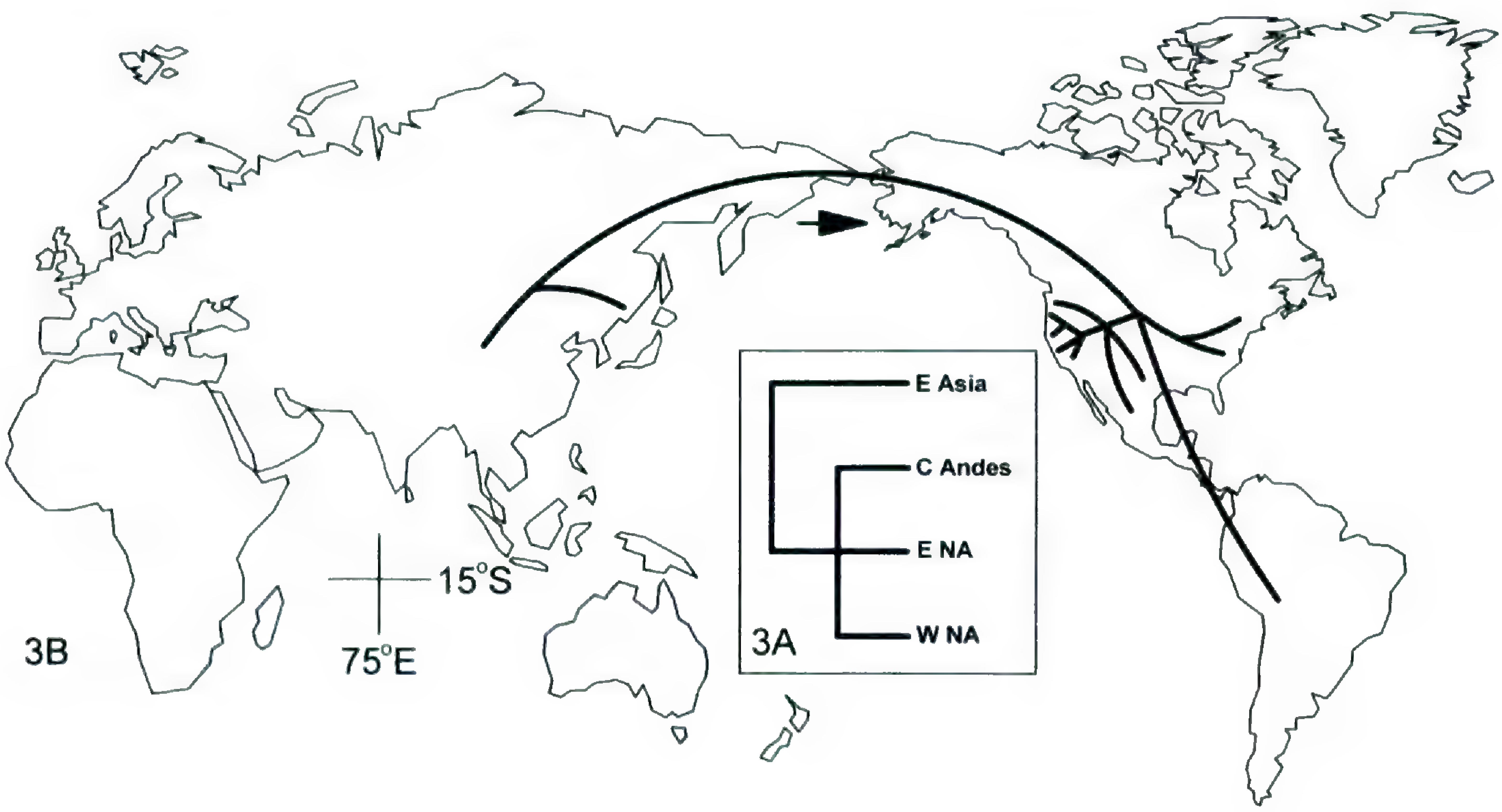

Figure 3. Biogeography of *Osmorhiza*.—A. Area cladogram of *Osmorhiza* based on the nuclear ribosomal ITS phylogeny. —B. Model of diversification in *Osmorhiza*.

statistically significant at the 5% level, whereas eight species pairs showed significant differences. These tests suggest that *O. berteroi* had a slower rate of nucleotide substitutions in the ITS regions than *O. aristata*, *O. depauperata*, *O. mexicana*, and *O. occidentalis*. They also show that *O. glabrata* had a slower rate of nucleotide substitution than *O. aristata*, *O. depauperata*, *O. mexicana*, and *O. occidentalis*. The molecular clock hypothesis for the ITS sequences in *Osmorhiza* was therefore rejected.

AREA CLADOGRAM CONSTRUCTION

The area cladogram (Fig. 3A) was constructed with the MPT and MLT using the optimality method in COMPONENT (vers. 2.0, Page, 1993). Among the four areas of endemism, Asia is basal and eastern North America, western North America, and central Andes form a trichotomy.

Discussion

PHYLOGENY AND PATTERNS OF DIFFERENTIATION

Parsimony and maximum likelihood analyses support the basal position of the Asian *O. aristata* within the genus and the monophyly of the New World taxa; these relationships were previously suggested in Downie et al. (2000) in a broader analysis of the tribe Scandiceae of Apiaceae. Within the New World species, three major subclades are suggested: (1) the eastern North American *O. claytonii* and *O. longistylis*; (2) a largely western North American clade comprising *O. berteroi*, *O. brachypoda*, *O. depauperata*, *O. mexicana*, *O. occidentalis*, and *O. purpurea*; and (3) the central Andean endemic *O. glabrata*. The neighbor-joining tree, however, groups the central Andean endemic *O. glabrata* with the eastern North American *O. claytonii* and *O. longistylis*. The *O. claytonii*–*O. longistylis*–*O. glabrata* group is then sister to *O. aristata* from Asia. As in the MPT and the MLT, the NJT also suggests a largely western North American group comprising *O. berteroi*, *O. brachypoda*, *O. depauperata*, *O. mexicana*, *O. occidentalis*, and *O. purpurea*.

The ITS phylogeny conflicts in several aspects with the phylogenetic hypothesis implied in the infrageneric classification of Lowry and Jones (1984) based on morphology (cf. Table 1). *Osmorhiza occidentalis* is a morphologically distinct species and was thus originally described in the monotypic genus *Glycosma* by Nuttall (in Torrey & Gray, 1840). Recent treatments have included this species within *Osmorhiza*, but placed it in its own section (Constance & Shan, 1948) or subgenus (Lowry & Jones, 1984) because of the numerous features that distinguish it from other members of the genus, including glabrous fruits lacking a caudate appendage, numerous staminate umbellules and flowers, bipinnate leaves, and yellow to greenish yellow flowers. The inclusion of *O. occidentalis* within a well-supported western North American clade in the ITS phylogeny suggests, however, that its dis-

tinctive morphological characters are most likely attributable to rapid evolution within the species, resulting in many autapomorphies.

Another discrepancy between the current infrageneric classification and the ITS phylogeny involves the three species currently included in *Osmorhiza* sect. *Osmorhiza*: the Asian *O. aristata* and the eastern North American *O. claytonii* and *O. longistylis*. These taxa form a morphologically coherent group and were even treated as a single species by some authors (e.g., Gray, 1859; Clarke, 1879; Kuntze, 1891; Boivin, 1968). They share several diagnostic features, including an involucre composed of (1–)2–3(–5) conspicuous, foliaceous bractlets, and styles (including the high-conic stylopodium) that are 1–3.6 mm long. However, based on ITS data, *O. aristata* is not only basal within the genus, but also shows a high level of sequence divergence from its congeners (1.627–3.784%), suggesting its early divergence within the group. The relative antiquity of *O. aristata* and the comparatively high level of morphological similarity between it and the eastern North American species are consistent with the hypothesis of morphological stasis among eastern Asian–eastern North American disjuncts, as proposed by Parks and Wendel (1990). Taxa of the eastern North American clade are sister to the western North American clade and not to *O. aristata*. The morphological similarity between *O. aristata*, *O. claytonii*, and *O. longistylis* could, however, be explained by their having experienced morphological stasis while concurrently the largely western North American clade diversified more rapidly.

Morphological stasis was first proposed by Parks and Wendel (1990) as a possible explanation for the presence of morphological similarities among eastern Asian–eastern North American disjunct taxa that are not closely related or do not represent sister groups. They found that two morphologically similar disjunct species of *Liriodendron* (*L. chinense* (Hemsley) Sargent and *L. tulipifera* L.) show a high level of allozyme and cpDNA divergence. Molecular and fossil data suggest the divergence time of the two species to be 10–16 million years ago (middle Miocene). Morphological stasis has also been suggested to explain similarities between the Asian and North American species of *Aralia* sect. *Dimorphanthus* (Wen, 2000), *Liquidambar* (Hoey & Parks, 1991; Shi et al., 1998), and *Magnolia* sect. *Rytidospermum* (Qiu et al., 1995a, 1995b).

A third conflict between the current infrageneric classification of *Osmorhiza* and the ITS data involves the central Andean endemic *O. glabrata*. The relationships and taxonomic placement of this species have been somewhat ambiguous. Constance and Shan (1948) included *O. glabrata* in their section "*Glycosmae*" along with *O. occidentalis*, largely based on apparent similarities in their fruits. By contrast, Lowry and Jones (1984) placed the Andean endemic in section *Mexicanae*, which also comprises *O. brachypoda* and *O. mexicana*. Shared characters among these species include short styles (0.5–1.2 mm long), a low-conic stylopodium, a conspicuous involucre of 1–6 bractlets, and an absent or poorly developed involucel subtending the umbellules. By contrast, the maximum parsimony and the maximum likelihood analyses suggest that *O. glabrata* forms a trichotomy with the eastern North American clade (*O. claytonii* and *O. longistylis*) and the largely western North American clade. The neighbor-joining tree, however, places *O. glabrata* sister to the eastern North American *O. claytonii*–*O. longistylis* group. The ITS phylogeny (Fig. 2) thus suggests the relative antiquity of *O. glabrata* among the New World species. It seems most plausible that *O. glabrata* was derived from a North American ancestor, perhaps shared with *O. claytonii* and *O. longistylis* (as in the NJT) or with taxa of the eastern North American clade and the western North American clade (Fig. 2). The present narrow distribution of *O. glabrata* in the central Andes may be due to local survival following the Pleistocene glaciations, which have been considered important in the evolution of the Andean flora (Vuilleumier, 1971; Simpson, 1975, 1983; Prance, 1982). Additional data are, however, needed to ascertain the exact phylogenetic position of *O. glabrata*.

INFRASPECIFIC VARIATION

Differentiation within O. occidentalis. *Osmorhiza occidentalis* showed a relatively high level of infraspecific sequence divergence, with a Kimura two-parameter distance of 1.013% between populations from the Rocky Mountains and California. Morphologically, *O. occidentalis* is somewhat variable, and several segregate species have been recognized in the past based primarily on differences in inflorescence structure, leaf pubescence, and fruit size (see Lowry & Jones, 1984). These differences, however, were regarded as minor by Lowry and Jones (1984), who provided data showing that a broadly defined *O. occidentalis* comprises a morphologically coherent group despite the presence of a few rather atypical collections (some of which served as the basis for the segregate species). Because *O. occidentalis* is so distinct from its congeners, it may be that infraspecific morphological variation has been over-

looked by previous workers. Additional studies should be undertaken to re-assess variability within *O. occidentalis* and to evaluate whether the molecular divergence is correlated with morphology and/or geographic distribution.

Differentiation between O. mexicana *subsp.* mexicana *and subsp.* bipatriata. The two subspecies of *O. mexicana* show a relatively high level of ITS sequence divergence (1.415%). Moreover, they did not form a monophyletic group in the phylogenetic analysis (Fig. 2). Initially, Constance and Shan (1948) recognized these taxa as distinct species, but Lowry and Jones (1984) treated them as subspecies because of the presence of occasional morphological intermediates at several localities in northern Mexico, including one area (Cerro Poposí, Nuevo León) where they co-occur with typical material of both subspecies. The biphyly of *O. mexicana*, as currently circumscribed, suggests the need to reexamine the status of subspecies *bipatriata* and the possible causes of the morphological intermediates. Although no interspecific hybridization has been reported for *Osmorhiza*, occasional morphological intermediates have been observed in sympatric populations of *O. berteroi* and *O. occidentalis* in western Oregon (R. Halse, pers. comm.).

BIOGEOGRAPHY

Diversification in major geographic areas. The ITS phylogeny (Fig. 2) shows that rates of cladogenesis vary among the four major areas occupied by *Osmorhiza*: eastern Asia, eastern North America, western North America, and the central Andes. Cladogenesis clearly appears to have been more rapid in the New World than in Asia, and the western North American clade shows a particularly high level of species diversity (Fig. 3B). It is unusual that Asia is species-depauperate considering that most other Asian–North American disjunct genera show a higher species diversity there (Tiffney, 1985; Wen, 1999). The number of *Osmorhiza* species occurring in each area may in part be the result of differential rates of extinction, especially during the Quaternary glaciations. However, it is generally accepted that North America was more severely affected by glaciation than eastern Asia due to its more complex topography and the north–south rather than primarily east–west orientation of its mountain ranges (Axelrod et al., 1998; Wen, 1999).

Western North America is the center of species diversity in *Osmorhiza*, with six of the ten species occurring in this region. The monophyly of the western North American clade is well supported in all three analyses presented here. Morphologically, however, the clade is rather diverse, with members from both subgenera and two of the three sections recognized by Lowry and Jones (1984). The ITS phylogeny suggests two successive diversifications within *Osmorhiza* in western North America. First, the common ancestor of the western North American clade may have diversified into *O. berteroi*, *O. mexicana*, and the ancestor of the *O. brachypoda–O. depauperata–O. occidentalis–O. purpurea* subclade. The latter subclade then appears to have differentiated further. This diversification among western North American *Osmorhiza* may have been highly influenced by the availability of a range of habitats associated with the uplifting of the Rocky Mountains and the western cordillera during the Tertiary (Barbour & Christensen, 1993; Graham, 1993).

The Andean endemic *O. glabrata* most likely represents an isolated relict. Its phylogenetic position is not well-resolved in the ITS phylogeny. It may have diverged rapidly early in the evolutionary history of the North American *Osmorhiza*, persisting in a relatively small portion of the central Andes. The fruits of *O. glabrata* are glabrous to sparsely hispid, which may afford them limited opportunities for long-distance dispersal by animals. It should be noted, however, that *O. occidentalis* almost always has completely glabrous fruits but nevertheless extends throughout a much larger area of western North America (Lowry & Jones, 1984).

Eastern Asian–eastern North American disjunction. The relative antiquity of the eastern Asian–eastern North American disjunction in *Osmorhiza* is suggested by the phylogenetically basal position of the Asiatic *O. aristata*, the monophyly of the diverse New World species (Fig. 2), and the relatively high ITS sequence divergence between *O. aristata* and its congeners. The most commonly accepted interpretation of the origin of eastern Asian–eastern North American disjunctions is that this pattern reflects an initial widespread distribution of temperate forest elements in the Northern Hemisphere during the mid Tertiary followed by subsequent extirpations in western North America and western Europe as a result of late Tertiary and Quaternary climatic cooling (Graham, 1993; Manchester, 1999; Wen, 1999). No fossils of *Osmorhiza* have been reported that could help to date the biogeographic disjunction. Also, the rejection of the molecular clock hypothesis for the ITS sequences in *Osmorhiza* (see Results) makes it questionable to attempt an indirect estimate of the times of divergence between the eastern Asian and the North American members of the genus.

The apparent close relatives of *Osmorhiza*, the genera *Myrrhis* and *Geocaryum* (Downie et al., 2000), are restricted to the Old World, which is consistent with a hypothesized Old World origin of *Osmorhiza* (Downie et al., 2000). The basal position of the Asian *O. aristata* and the Old World distribution of *Myrrhis* and *Geocaryum* are consistent with the idea that the ancestor of the North American *Osmorhiza* migrated from Asia.

American antitropical disjunction. *Osmorhiza berteroi* and *O. depauperata* show a similar pattern of antitropical disjunction between western North America and temperate South America. Constance (1963) suggested that these species may have migrated south in a step-wise manner along the western American cordillera throughout the Tertiary, with subsequent elimination of populations from intervening tropical areas. The present-day distribution of *O. mexicana* subsp. *mexicana*, which comprises isolated populations that bridge the areas currently occupied by *O. berteroi* and *O. depauperata*, appears to support the idea that the now-disjunct species could also have had a more continuous distribution in the past. However, the absence of ITS sequence divergence between the western North American and South American populations of both species suggests a recent origin of the observed antitropical disjunctions. Species of *Osmorhiza* are facultatively autogamous, which would enable establishment of a new population from a single propagule, and their armed fruits with caudate appendages and numerous retrorse bristles appear to be well adapted for epizoochorous dispersal (Lowry & Jones, 1984). As indicated by Raven (1963), the pattern of disjunction of temperate taxa between western North America and southern South America corresponds closely to the migration routes of many bird species, and this probably accounts for the disjunctions seen in *O. berteroi* and *O. depauperata* (Lowry & Jones, 1984). Thus, the lack of ITS sequence divergence, the monophyly of both species, and their fruit morphology are all consistent with an origin of the antitropical disjunction due to relatively recent long-distance dispersal via birds from western North America to South America. A similar explanation has been used for several disjunct taxa of grasses (Peterson & Morrone, 1997; Peterson & Ortíz-Diaz, 1998).

Eastern–western North American disjunction. The phytogeographic disjunction between western North America, the Great Lakes region, and northeastern North America has been discussed repeatedly since it was first reported by Fernald in 1925 (Fernald, 1925, 1935; see also Stebbins, 1935; Rousseau, 1953; Drury, 1969; Schofield, 1969; Morisset, 1971; Voss, 1972; Wood, 1972; Miller & Thompson, 1979). It is now generally regarded that the disjunct populations of species showing this pattern are remnants of a previously widespread flora that probably survived south of the glacial boundaries, but perhaps also in nunataks (cf. Fernald, 1925), and then migrated to their present sites following the Pleistocene, while being eliminated from the refugia in the south (Schofield, 1969; Miller & Thompson, 1979). In explaining the western North American–eastern North American disjunctions in *O. berteroi* and *O. depauperata*, Lowry and Jones (1984) also emphasized that taxa occurring in the Great Lakes area and the northeast are most likely now restricted to sites with less competition from eastern boreal taxa and where climatic conditions are similar to those in western parts of the continent. In the present study, the western cordilleran populations of *O. berteroi* showed an identical ITS profile to those of the Great Lakes region, while the eastern populations had just a single nucleotide substitution. The fact that there is little or no sequence divergence within each of these species is consistent with a relatively recent origin of the disjunct pattern during the glacial or postglacial periods.

PHYSIOLOGICAL ADAPTATION—SEED DORMANCY

Disjunct species of herbaceous plants with relict distributions in both eastern North America and Asia appear to exhibit stasis in ecological traits (Ricklefs & Latham, 1992). Similarly, closely related species groups with members occurring in one or the other area may also show stasis with regard to various traits, including the type of morphophysiological dormancy (MPD) they exhibit. This is the case for seeds of the eastern North American–Asian disjunct species pairs *Jeffersonia diphylla* (L.) Pers.–*J. dubia* (Maxim.) Benth. & Hook. f. (Berberidaceae) and *Panax quinquefolius* L.–*P. ginseng* C. A. Meyer (Araliaceae), all of which have deep simple MPD (cf. Baskin & Baskin, 1998). In *Osmorhiza*, however, seeds of *O. aristata* from Asia and *O. berteroi* and *O. occidentalis* from western North America share the same type of MPD (deep complex MPD), whereas those of the eastern North American *O. claytonii* and *O. longistylis* exhibit a different type of dormancy (nondeep complex MPD). Wake et al. (1983) suggested that changes in some traits, including physiological ones, might help an organism to compensate for maintaining a stable morphology over long periods of time. This would appear to be the case in members of *Osmorhiza*.

Although much additional work must be completed before we have a robust understanding of the evolution of various types of MPD, some insights into their evolution may be drawn from the phylogeny of *Osmorhiza*. The plesiomorphic condition in the genus appears to be deep complex MPD, whereas nondeep complex MPD is derived. This is further supported by studies that show seeds of the outgroup *Myrrhis odorata* also have deep complex MPD (Lhotska, 1977; Deno, 1994). The suggestion of Baskin et al. (1995) that deep complex MPD may have been derived from nondeep complex MPD is not upheld according to the ITS phylogeny of *Osmorhiza*.

Seeds of most (and probably all) *Osmorhiza* species are dispersed during summer/autumn, with germination occurring in spring (Baskin & Baskin, 1984, 1991; Baskin et al., 1995; Walck et al., 2002). A cold stratification period would thus ensure that germination does not occur until the following spring, since dormancy is broken with cold (winter) stratification. The selective forces responsible for the evolution of the requirement for a warm stratification pretreatment prior to cold stratification observed in the eastern North American *O. claytonii* and *O. longistylis* are unclear. The most parsimonious explanation based on the ITS phylogeny is that the evolution of this trait occurred in the common ancestor of these closely related sister species. It seems reasonable, however, to assume that a common environmental selection pressure (or a set of pressures) was responsible for the acquisition of the warm + cold stratification requirement. Interestingly, species of *Erythronium* have a similar geographic pattern of MPD types, with seeds from the western North American *E. grandiflorum* Pursh exhibiting deep complex MPD and those from the eastern North American *E. albidum* Nutt. and *E. americanum* Ker Gawler showing nondeep complex MPD (Baskin et al., 1995).

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A SYNOPSIS OF *OCOTEA* (LAURACEAE) IN CENTRAL AMERICA AND SOUTHERN MEXICO[1]

Henk van der Werff[2]

Abstract

Ocotea is the largest genus of Lauraceae in Mesoamerica (Central America and Southern Mexico, i.e., the area between the Isthmus of Tehuantepec in Mexico and the Panamanian–Colombian border) with 102 species recognized. The most recent treatment of Mesoamerican *Ocotea* was published by Carolyn Allen in 1945. It included 33 species and is now seriously outdated. A synopsis of the genus as it is currently known from Mesoamerica is presented here, consisting of a key to species, synonymy, type information, some brief notes on characters useful in their identification, and distribution by country and altitude.

Key words: Central America, Lauraceae, Mesoamerica, *Ocotea*, southern Mexico.

Lauraceae are a large and ecologically important family of trees and shrubs in wet tropical forests from sea level to the tree line at about 3000 m. The family is rare or lacking in areas with a pronounced dry season. Lauraceae have the reputation of being a difficult family, partly because of problems with generic delimitation and partly because many species are trees with inconspicuous flowers and therefore difficult to find and are infrequently collected with flowers. A key to the genera of Lauraceae in the Neotropics was published by van der Werff (1991); this key was based on floral and vegetative characters but did not include fruit characters. Combining fruit and floral characters in a key makes it almost impossible to use because herbarium specimens do not as a rule have both flowers and fruits. By far the largest of the genera of Lauraceae in the New World is *Ocotea* Aubl., with an estimated 300+ species in the Neotropics (van der Werff, 1991) or 350 including the African and Madagascan species (Rohwer, 1993). *Ocotea* is characterized by its stamens with 4 locelli, these arranged in 2 pairs, unisexual or hermaphrodite flowers, a lack of papillae on the stamens or tepals in most species (papillae are present in a few species, but these have the locelli clearly arranged in 2 pairs), and the tepals free, not basally united, and falling off in old flowers or rarely persisting on the cupule. In this way *Ocotea* is not very well defined, and both van der Werff (1991) and Rohwer (1993) suggested that *Ocotea* serves as the catchall genus for species with 4-celled stamens that do not fit in the other, better-defined genera of Lauraceae. The Central American and Southern Mexican (from the area between the Isthmus of Tehuantepec in Mexico and the Panamanian–Colombian border, hereafter referred to as Mesoamerica) species of *Ocotea* were last revised by Allen (1945), who included 33 species in the genus. Since then, additional collections from Chiapas and Guatemala have led to the description of several new species by Lundell (1965, 1969, 1970, 1971, 1974a, 1974b, 1977, 1978). In the more recent treatment of Lauraceae for the *Flora Costaricensis* (Burger & van der Werff, 1990) 42 species of *Ocotea* were recognized, including 7 new species. Rohwer (1991) reviewed the marginal species of the *O. helicterifolia* group, including the *O. heydeana* group, and described four new species. Van der Werff (1999) treated the core species of the *O. helicterifolia* group and found four additional new species. The study of recent collections of Mesoamerican Lauraceae has resulted in publications in which new *Ocotea* species have been or will be described (Gomez-Laurito, 1993, 1997; Hammel, 1986; Lorea-Hernandez & van der Werff, 2002 in press; Nelson, 1984; van der Werff, 1987, 1988a, 1988b, 1996, 2001; Wendt, 1998; Wendt & van der Werff, 1987).

Species Groups in *Ocotea*

In a genus as diverse as *Ocotea*, one can expect to find several distinct species groups. Rohwer (1986) published an overview of the species of *Nec-*

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Table 1. *Ocotea* species with unisexual flowers in the Mesoamerican region.

Ocotea adela
Ocotea atlantica
Ocotea aurantiodora
Ocotea calophylla
Ocotea cernua
Ocotea fendleri
Ocotea floribunda
Ocotea leucoxylon
Ocotea macropoda
Ocotea oblonga
Ocotea puberula
Ocotea rubrinervis

tandra Roland. ex Rottb., *Ocotea, Pleurothyrium* Nees, and *Rhodostemonodaphne* Rohwer & Kubitzki, largely based on a study of type specimens. He recognized a number of species groups in *Ocotea* based on characters of flowers and fruits. Among the Mesoamerican species the following groups can be recognized, starting with the best-defined groups:

1. Species with unisexual flowers. This group comprises almost half the species of *Ocotea* and is best represented in South America. In Mesoamerica one finds 12 species of this group (Table 1). Most of those are also present in South America, and only two are endemic to Mesoamerica (*O. adela* van der Werff and *O. atlantica* van der Werff). Rohwer (1986) divided this group into numerous smaller groups, based largely on the South American species. The Mesoamerican species can all be confidently assigned to these smaller groups, but listing these would be too detailed for this synopsis.

2. *Ocotea* subg. *Dendrodaphne* (Beurl.) Mez. This group is characterized by a combination of the following characters: inflorescences in the axils of bracts near the tips of the twigs; cupules with a double-rimmed margin; flowers with spreading tepals; and nearly sessile, tongue-shaped stamens with a sterile tip and a papillose indument. This is a small, but well-defined group consisting of about 10 species, with 4 species in Mesoamerica (Table 2).

3. The *Ocotea helicterifolia* group. This group shares some characters with the species of *Ocotea* subg. *Dendrodaphne* and can be recognized by the following combination of characters: inflorescences in the axils of normal leaves; cupules with a single margin; flowers with spreading tepals and stamens subsessile or infrequently with a distinct filament, sometimes tongue-shaped, densely papillose and with a sterile tip or more commonly rectangular, without a sterile tip and very sparsely papillose.

Table 2. Species of *Ocotea* subg. *Dendrodaphne* in the Mesoamerican region.

Ocotea dendrodaphne
Ocotea klepperae
Ocotea morae
Ocotea veraguensis

This group has been recently revised by Rohwer (1991), who studied *O. heydeana* (Mez & J. D. Smith) Bernardi and its allies, which have glabrous or very sparsely pubescent leaves, and *O. sinuata* (Mez) Rohwer and its allies, which have densely pubescent leaves and densely papillose stamens with a sterile tip, as well as by van der Werff (1999), who studied *O. helicterifolia* (Meissner) Hemsley and its allies, characterized by pubescent leaves and stamens with few papillae, without a sterile tip. This group is strongly centered in Mesoamerica, with only one species in northern South America, and includes about 32 species (Table 3).

4. The *Ocotea insularis* group. This group is characterized by two seemingly insignificant characters. One is the pubescence of the inner 3 sta-

Table 3. Species of the *Ocotea helicterifolia* group in the Mesoamerican region.

1. *Ocotea acuminatissima*
2. *Ocotea arcuata*
3. *Ocotea bajapazensis*
4. *Ocotea betazensis*
5. *Ocotea botrantha*
6. *Ocotea bourgeauviana*
7. *Ocotea brenesii*
8. *Ocotea congregata*
9. *Ocotea corrugata*
10. *Ocotea gordonii*
11. *Ocotea helicterifolia*
12. *Ocotea heydeana*
13. *Ocotea holdridgeiana*
14. *Ocotea lentii*
15. *Ocotea magnifolia*
16. *Ocotea mollicella*
17. *Ocotea patula*
18. *Ocotea pausiaca*
19. *Ocotea pharomachrosorum*
20. *Ocotea pittieri*
21. *Ocotea platyphylla*
22. *Ocotea praetermissa*
23. *Ocotea purpurea*
24. *Ocotea rhytidotricha*
25. *Ocotea rubriflora*
26. *Ocotea sinuata*
27. *Ocotea tonii*
28. *Ocotea valeriana*
29. *Ocotea valerioides*
30. *Ocotea verticillata*
31. *Ocotea sp. A.*

Table 4. Species of the *Ocotea insularis* group in the Mesoamerican region.

1.	*Ocotea atirrensis*
2.	*Ocotea austinii*
3.	*Ocotea barbatula*
4.	*Ocotea chiapensis*
5.	*Ocotea contrerasii*
6.	*Ocotea endresiana*
7.	*Ocotea glaucosericea*
8.	*Ocotea insularis*
9.	*Ocotea jefensis*
10.	*Ocotea laetevirens*
11.	*Ocotea meziana*
12.	*Ocotea producta*
13.	*Ocotea rivularis*
14.	*Ocotea rovirosae*
15.	*Ocotea whitei*
16.	*Ocotea viridiflora*

mens; these stamens have a patch of white hairs on the side facing the pistil at the junction of the filament and the anther. The second character is found in the inflorescence: the secondary, tertiary, and further branches of the inflorescence are flattened, with the axis of flattening of the tertiary branches forming a 90° angle with those of the secondary branches, those of the quaternary branches forming a 90° angle with the tertiary branches, and so on. In other characters this group conforms to the general *Ocotea* pattern: inflorescences in the axils of leaves; cupules with a single margin; flowers with erect to half-erect tepals and stamens with a distinct filament, not papillose, and without a sterile tip. This group is best represented in Mesoamerica, with one or a few species in northern South America. I would place 16 Mesoamerican species in this group (Table 4), including *O. meziana* C. K. Allen and its allies, which differ from the *O. insularis* group mainly in the light green drying leaves with raised reticulation and often yellowish major veins. My concept of this group is considerably wider than that of Rohwer (1986).

Beyond these reasonably well-defined, larger groups one can establish a larger number of poorly defined, small groups, but doing so is beyond the scope of this synopsis. Too many species would be transitional between such groups, and they would contribute little to our understanding.

If *Ocotea* is the genus to which all species that cannot be placed in other, better-defined genera of Lauraceae are assigned, one may ask if *Ocotea*, as currently accepted, is monophyletic. The answer to this question can be drawn from a recent DNA-based phylogeny of Lauraceae (Chanderbali et al., 2001). In this study 22 species of *Ocotea*, representing several different groups, were included. Those results show clearly that *Ocotea* is not a monophyletic genus, but that the following clades can be recognized:

1. The 9 species with unisexual flowers formed a clade together with *Endlicheria* Nees and *Rhodostemonodaphne*, both genera with unisexual flowers.
2. The 3 species of the *O. helicterifolia* group formed a clade.
3. The 2 species of subgenus *Dendrodaphne* formed a clade.
4. The 4 Old World species formed a clade.
5. Three species with perfect flowers (including *O. insularis* (Meissner) Mez) formed a clade with 3 *Aniba* species and 1 *Aiouea* species.
6. A recently described species from Cameroon, *O. ikonyopke* van der Werff, was part of a clade with *Cinnamomum* species and was probably incorrectly placed in *Ocotea*.

These clades are well separated from one another, and maintaining *Ocotea* as a monophyletic genus would require a transfer of several quite distinct genera (such as *Nectandra*, *Pleurothyrium*, *Aniba* Aubl., *Licaria* Aubl.) into *Ocotea*, a solution that I do not find acceptable. Hence *Ocotea* should be considered a polyphyletic genus. Mez (1889) recognized 198 species in *Ocotea* and divided the genus into 4 subgenera: subg. *Hemiocotea* Mez, with 1 species, now placed in the genus *Urbanodendron* Mez; subg. *Dendrodaphne*, 8 species, with the same circumscription as it currently has; subg. *Mespilodaphne* (Nees) Mez, consisting of all remaining species (51) with perfect flowers; and subg. *Oreodaphne* (Nees) Mez, including all species (138) with unisexual flowers. The DNA study supports the monophyly of subgenera *Dendrodaphne* and *Oreodaphne*, but not of subgenus *Mespilodaphne*. Morphological characters for a division of subgenus *Mespilodaphne* in monophyletic groups have not yet been found.

This synopsis is based on a treatment of *Ocotea* for the *Flora Mesoamericana* and includes the 102 species found from the Isthmus of Tehuantepec in Mexico south to the border between Panama and Colombia. Mexican species only known from the area north of the Isthmus of Tehuantepec are not included. Altitudinal distribution for species also occurring outside of Mesoamerica is based on Mesoamerican specimens and does not reflect their altitudinal distribution outside this area.

KEY TO THE SPECIES OF *OCOTEA* IN MESOAMERICA

1. Stamens tongue-shaped, with a distinct, sterile tip, moderately to densely papillose; filaments lacking or very short 2
1'. Stamens not tongue-shaped, usually rectangular, without a sterile tip, not papillose or rarely with papillae on the margin; filaments usually present 11
2(1). Lowermost pair of lateral veins with conspicuous pocket domatia .... 41. *O. holdridgeiana*
2'. Leaves without conspicuous pocket domatia 3
3(2). Twigs and usually the leaves densely pubescent 4
3'. Twigs and leaves glabrous or nearly so 8
4(3). Leaves clustered .... 99. *O. verticillata*
4'. Leaves evenly distributed along the twigs 5
5(4). Lower leaf surface completely covered by the indument, the hairs short and curled .... 66. *O. pharomachrosorum*
5'. Lower leaf surface not completely covered by the indument, but partly or almost completely visible 6
6(5). Leaves elliptic, to 6 cm wide; petioles 5–9 mm long .... 46. *O. klepperae*
6'. Leaves obovate or obovate-elliptic, 5–17 cm wide; petioles 1.5–4 cm long 7
7(6). Inflorescences paniculate-cymose; pistils densely pubescent .... 84. *O. sinuata*
7'. Inforescences racemose; pistils glabrous .... 13. *O. botrantha*
8(3). Twigs hollow 9
8'. Twigs solid 10
9(8). Shrubs or small trees to 8 m; leaf bases plane, not revolute; inflorescences to 15 cm long; fruits ca. 2 × 1 cm; cupule ca. 1 cm diam., cup- to bowl-shaped, very weakly double-margined, the outer margin ca. 0.5 mm wide; widespread .... 24. *O. dendrodaphne*
9'. Trees to 20 m; leaf bases slightly revolute; inflorescences to 5 cm long; fruits ca. 5 × 3.5 cm, cupule ca. 5 cm diam., bowl-shaped, with a conspicuous double margin, this ca. 1 cm wide; Costa Rica .... 58. *O. morae*
10(8). Inflorescences about as long as the leaves, sparsely pubescent; leaf bases plane, not revolute; fruits 2 × 1 cm, cupule to 1.2 cm diam., with a double margin, the outer margin ca. 2 mm wide; widespread .... 97. *O. veraguensis*
10'. Inflorescences much shorter than the leaves, densely pubescent; leaf bases slightly revolute; fruits ca. 5 × 3.5 cm, cupule ca. 5 cm diam., with a conspicuous double margin, this ca. 1 cm wide; Costa Rica .... 58. *O. morae*
11(1). Lower leaf surface completely hidden by the indument 12
11'. Lower leaf surface glabrous or partly covered by the indument 17
12(11). Flowers unisexual; leaf base inrolled and decurrent along the entire length of the petiole; vernation lines visible on the lower leaf surface .... 16. *O. calophylla*
12'. Flowers perfect; leaf base plane or if inrolled and decurrent, most of the petiole distinct; vernation lines not present 13
13(12). Leaf base inrolled and shortly decurrent on the petiole .... 83. *O. salvinii*
13'. Leaf base plane and not decurrent 14
14(13). Indument of the lower leaf surface pale brown or whitish 15
14'. Indument of the lower leaf surface reddish brown 16
15(14). Domatia absent; flowers 6 mm diam., tepals 2–2.5 mm long .... 82. *O. salvadorensis*
15'. Domatia present as axillary tufts of hairs; flowers 4 mm diam., tepals 1.5 mm long .... 43. *O. iridescens*
16(14). Receptacle glabrous inside; tepals papillose on the inner surface; leaves 9–16 cm long .... 81. *O. rufescens*
16'. Receptacle appressed pubescent inside; tepals pubescent on the inner surface; leaves 7–10 cm long .... see discussion under 82. *O. salvadorensis*
17(11). Twigs hollow, often inhabited by ants 18
17'. Twigs solid 19
18(17). Inflorescences and flowers densely brown-tomentellous; leaves broadly obovate, coriaceous, with raised reticulation .... 44. *O. jefensis*
18'. Inflorescences and flowers glabrous or sparsely puberulous; leaves (narrowly) elliptic or obovate, (firmly) chartaceous, reticulation immersed or raised .... 5. *O. atirrensis*
19(17). Flowers unisexual 20
19'. Flowers perfect 30
20(19). Lower leaf surface with erect hairs, discernable to the touch 21
20'. Lower leaf surface glabrous or with appressed hairs, hairs not discernable to the touch 23
21(20). Indument completely covering the surface of the twigs 22
21'. Surface of the twigs partially visible between the hairs .... 51. *O. macropoda*
22(21). Laminae slightly decurrent on the petiole; laminae and petioles not sharply offset; tertiary venation on the lower leaf surface scalariform and clearly raised; indument on young twigs shaggy .... 30. *O. fendleri*
22'. Base of laminae obtuse, clearly differentiated from the petiole; tertiary venation on lower leaf surface scarcely raised and not scalariform; indument on young twigs very short, erect .... 6. *O. atlantica*
23(20). Twigs sharply angular; upper leaf surface with raised, minute reticulation .... 7. *O. aurantiodora*
23'. Twigs rounded or slightly angular; upper leaf surface without raised reticulation or with coarse reticulation 24

24(23). Pistils pubescent; cupules plate-like, with a double margin ... 31. *O. floribunda*
24′. Pistils glabrous; cupules various, but not plate-like and with a double margin ... 25
25(24). Pit domatia present in the axils of the lateral veins of some leaves, the domatia not pubescent ... 61. *O. oblonga*
25′. Pit domatia absent, but axillary tufts of hairs sometimes present ... 26
26(25). Axillary tufts of hairs present on the lower leaf surface; tepals persistent on the cupule; oil glands readily visible on the upper leaf surface as black dots ... 80. *O. rubrinervis*
26′. Axillary tufts of hairs lacking; tepals deciduous or persistent in fruit; oil glands not or scarcely visible ... 27
27(26). Twigs densely and minutely gray appressed pubescent, the hairs small and scarcely individually visible; indument on the inflorescences and pedicels notably denser than on the flowers ... 49. *O. leucoxylon*
27′. Twigs sparsely pubescent, individual hairs visible, or glabrous; inflorescences and flowers glabrous or density of indument on flowers and inflorescences about the same ... 28
28(27). Filaments of the outer 6 stamens fused with the tepals; inflorescences and flowers glabrous ... 17. *O. cernua*
28′. Filaments of the outer 6 stamens free; inflorescences and/or flowers sparsely pubescent ... 29
29(28). Leaves 7–25 cm long, the tertiary venation slightly raised on the upper surface; lateral veins immersed on the upper surface ... 72. *O. puberula*
29′. Leaves 4–11 cm long, the tertiary venation immersed on the upper surface; lateral veins slightly impressed on the upper surface ... 2. *O. adela*
30(19). Lower leaf surfaces and young twigs with predominantly erect hairs, these discernable to the touch ... 31
30′. Lower leaf surfaces and young twigs glabrous or with predominantly appressed hairs, rarely with sparse erect hairs, but these not discernable to the touch ... 55
31(30). Leaf bases decurrent on the petiole and usually inrolled ... 32
31′. Leaf bases not decurrent on the petiole, usually flat ... 35
32(31). Young twigs appressed pubescent, the indument moderate or sparse and part of the surface always visible; inner surface of tepals glabrous or nearly so ... 25. *O. dentata*
32′. Young twigs with erect or ascending hairs, the surface (nearly) completely covered; inner surface of tepals pubescent ... 33
33(32). Leaf bases prominently recurved; lateral veins 9 to 12 pairs ... 86. *O. stenoneura*
33′. Leaf bases scarcely if at all recurved or inrolled; lateral veins 4 to 8 pairs ... 34
34(33). Indument on lower leaf surface predominantly erect; leaves 10–20 cm long ... 37. *O. hartshorniana*
34′. Indument on lower leaf surface predominantly appressed; leaves 5–12 cm long ... 57. *O. monteverdensis*
35(31). Outer surface of tepals densely pubescent, the surface completely covered by the indument; if inner 3 tepals with less indument on the upper half, then at least outer 3 tepals densely pubescent ... 36
35′. Outer surface of all tepals glabrous or variously pubescent; if variously pubescent, the surface of the tepals always partially visible ... 40
36(35). Flowers 10–14 mm diam ... 33. *O. gomezii*
36′. Flowers less than 8 mm diam ... 37
37(36). Inflorescences few-flowered, racemose or with some lateral branches ending in a cyme; leaves coriaceous ... 71. *O. pseudopalmana*
37′. Inflorescences many-flowered, the lateral branches several times divided; leaves coriaceous or chartaceous ... 38
38(37). Petioles ca. 30 mm long ... 3. *O. amplifolia*
38′. Petioles up to 15 mm long ... 39
39(38). Leaves coriaceous, densely ferruginous pubescent on the lower surface; cupule with entire margin; leaf apex obtuse or very shortly acuminate ... 23. *O. darcyi*
39′. Leaves chartaceous, moderately to sparsely golden brown pubescent on the lower surface; tepals persisting on the cupule; leaf apex acuminate ... 56. *O. mollifolia*
40(35). Inflorescences racemose or rarely with a few lateral cymes ... 41
40′. Inflorescences paniculate-cymose ... 44
41(40). Midvein, lateral veins, and tertiary venation clearly impressed (leaves rugose-bullate) ... 22. *O. corrugata*
41′. Venation immersed or raised, not impressed (leaves not rugose-bullate) ... 42
42(41). Outer surface of tepals glabrous; anthers sessile ... 34. *O. gordonii*
42′. Outer surface of tepals (sparsely) pubescent; stamens with filaments ⅓ or more of the length of the anthers ... 43
43(42). Hairs on the lower surface of leaves ascending, covering most of the lamina; indument gray ... 55. *O. mollicella*
43′. Hairs on the lower leaf surface erect, most of the lamina visible; indument brown or ferruginous ... 74. *O. purpurea*
44(40). Leaves clustered ... 45
44′. Leaves alternate, evenly distributed along the twigs ... 47
45(44). Outer surface of the tepals glabrous ... 14. *O. bourgeauviana*
45′. Outer surface of the tepals pubescent ... 46
46(45). Petioles to 6 mm long; leaves 15–25 × 5–6 cm; indument of twigs yellow-brown ... 91. *O. tonii*
46′. Petioles at least 10 mm long; leaves 10–15 × 6–7 cm; indument of twigs brown ... 20. *O. congregata*

47(44). Flowers at anthesis 2–3 mm diam.; tepals erect to half-erect; inner surface of tepals and stamens glabrous .... 62. *O. oblongifolia*
47′. Flowers at anthesis 5–10 mm diam.; tepals spreading or half-erect; inner surface of tepals and/or stamens partially papillose or pubescent 48
48(47). Receptacle pubescent inside 49
48′. Receptacle glabrous inside 51
49(48). Leaves elliptic, to 15 cm long .... 12. *O. betazensis*
49′. Leaves obovate, 20–40 cm long 50
50(49). Indument completely covering young twigs and inflorescences .... 95. *O. valerioides*
50′. Surface of twigs and inflorescences visible between the indument .... 48. *O. lentii*
51(48). Outer surface of the tepals pubescent .... 64. *O. patula*
51′. Outer surface of the tepals glabrous 52
52(51). Inner surface of the tepals pubescent; filaments distinct, ca. ⅓ the length of the anthers 53
52′. Inner surface of the tepals glabrous; filaments not evident 54
53(52). Leaves to 10 cm long, the tips obtuse, acute or shortly acuminate .... 69. *O. praetermissa*
53′. Leaves 10–20 cm long, acuminate or gradually narrowed into a slender tip .... 14. *O. bourgeauviana*
54(52). Surface of young twigs completely covered by the indument; cupule cup-shaped .... 94. *O. valeriana*
54′. Surface of young twigs partially visible between the indument; cupule shallowly bowl-shaped or plate-like .... 38. *O. helicterifolia*
55(30). Leaf bases inrolled and/or decurrent on the petiole or reflexed, or leaves subsessile with the base weakly recurved; free petiole usually absent or very short 56
55′. Leaf bases not inrolled or decurrent on the petiole; petioles usually distinct 65
56(55). Flowers densely reddish pubescent; terminal buds glabrous or finely appressed pubescent distally .... 90. *O. tonduzii*
56′. Flowers gray pubescent or glabrous; terminal buds uniformly pubescent or rarely glabrous 57
57(56). Leaves usually 30–50 cm long, the apex usually rounded; domatia lacking .... 77. *O. rivularis*
57′. Leaves usually less than 25 cm long, apices obtuse or rounded; domatia lacking or present 58
58(57). Leaf bases reflexed, the lobes frequently covering the midrib; flowers glabrous .... 27. *O. endresiana*
58′. Leaf bases decurrent or inrolled, but not reflexed; flowers usually puberulous 59
59(58). Flowers 4–5 mm diam 60
59′. Flowers 2.5–3 mm diam 61
60(59). Outer surface of the tepals densely whitish pubescent, the surface completely covered; vernation lines visible on the lower leaf surface; receptacle (deeply) cup-shaped; Costa Rica, Panama .... 32. *O. glaucosericea*
60′. Outer surface of the tepals moderately pubescent, the surface partly visible; vernation lines not visible; receptacle bowl-shaped; Mexico, Guatemala .... 18. *O. chiapensis*
61(59). Leaves 5–10 cm wide, obovate, glabrous or with a few appressed hairs on the lower leaf surface; tertiary venation not or scarcely raised on upper leaf surface .... 42. *O. insularis*
61′. Leaves to 5 cm wide, elliptic or oblong, appressed pubescent or glabrous on the lower leaf surface; tertiary venation immersed or raised 62
62(61). Leaf base cuneate or acute, moderately or weakly reflexed, not decurrent on the petiole; leaves subsessile .... 42. *O. insularis* s.l.
62′. Leaf base decurrent on the petiole, usually inrolled; leaves petiolate 63
63(62). Tertiary venation raised on the upper surface; leaf tips obtuse; leaf bases inrolled and decurrent .... 8. *O. austinii*
63′. Tertiary venation not or rarely raised on the upper surface; if raised, leaf tips acute or acuminate and/or leaf bases decurrent, but not inrolled 64
64(63). Apparent petiole due to decurrent leaf bases, 4–5 cm long; flowers sparsely pubescent .... 70. *O. producta*
64′. Apparent petiole to 3 cm long, usually shorter; indument of flowers various .... 101. *O. whitei*
65(55). Tepals papillose or partially papillose on the inner surface; tepals glabrous or sparsely puberulent outside; tepals spreading at anthesis; tepals usually longer than 3 mm 66
65′. Tepals glabrous or pubescent on the inner surface; outer surface glabrous or variously pubescent; tepals usually erect or half-erect at anthesis; tepals usually less than 3 mm long 79
66(65). Hairs on the lower leaf surface erect (check along midrib and lateral veins) 67
66′. Hairs on lower leaf surface appressed or lacking 68
67(66). Inflorescences racemose; young twigs densely pubescent with minute, erect hairs .... 67. *O. pittieri*
67′. Inflorescences paniculate-cymose; young twigs moderately to densely appressed pubescent .... 76. *O. rhytidotricha*
68(66). Stamens with filaments at least as long as the anthers; outer stamens curved inward .... 65. *O. pausiaca*
68′. Stamens with filaments less than half as long as the anthers; outer stamens straight 69
69(68). Pit domatia present in the axils of the lowermost lateral veins .... 4. *O. arcuata*
69′. Pit domatia lacking, axillary tufts of hairs sometimes present 70
70(69). Inflorescences densely and minutely brownish pubescent, the surface covered or nearly so 71
70′. Inflorescences sparsely or moderately pubescent, the surface largely visible 72
71(70). Flowers 6–7 mm diam.; widespread, from southern Mexico to Panama .... 79. *O. rubriflora*
71′. Flowers 10–12 mm diam.; Osa Peninsula in Costa Rica .... 50. *O. macrantha*
72(70). Leaf margin at the base (narrowly) reflexed or inrolled .... 68. *O. platyphylla*

72′. Leaf margin at the base flat or nearly so ... 73
73(72). Inflorescences paniculate, with at least a few 3-flowered lateral cymes, rarely racemose but then with flowers 6.5 mm or more in diameter and leaves drying greenish ... 74
73′. Inflorescences racemose; leaves drying dark green or flowers less than 5 mm diam ... 77
74(73). Indument on twigs brown and ± persistent; indument on peduncle moderately dense ... 75
74′. Indument on twigs pale and becoming quickly sparse with age; indument on peduncle rather sparse ... 76
75(74). Lateral veins 6 to 9; Guatemala and Chiapas ... 52. *O. magnifolia*
75′. Lateral veins 4 to 5; Costa Rica ... 102. *Ocotea* sp. A
76(74). Flowers 4.5–5.5 mm diam.; lowlands ... 9. *O. bajapazensis*
76′. Flowers 6.5–9 mm diam.; montane forests, mostly above 900 m ... 40. *O. heydeana*
77(73). Indument on young twigs dense and consisting of short, erect hairs ... 67. *O. pittieri*
77′. Indument on young twigs of variable density and consisting of appressed, rarely somewhat ascending hairs ... 78
78(77). Receptacle densely pubescent inside; Costa Rica ... 15. *O. brenesii*
78′. Receptacle sparsely or very sparsely pubescent inside; Mexico, Guatemala ... 1. *O. acuminatissima*
79(65). Lower leaf surface with pit domatia, cavities with a small slit-like or rounded orifice, in the axils of the basal lateral veins or along the lower lateral veins; orifice usually glabrous, rarely with a fringe of hairs ... 80
79′. Lower leaf surface without pit domatia; axillary tufts of hairs in a small depression sometimes present ... 89
80(79). Domatia at least once, often several times, their diameter away from the midrib; three or more pairs of domatia present in each leaf; domatia with a fringe of hairs ... 10. *O. barbatula*
80′. Domatia adjacent to or less than their diameter away from the midrib; domatia present in the axils of several pairs of lateral veins or only in the axil of the basal pair; domatia usually glabrous ... 81
81(80). Flowers sparsely appressed pubescent; inflorescences moderately appressed pubescent ... 36. *O. haberi*
81′. Flowers glabrous; inflorescences glabrous or nearly so ... 82
82(81). Leaves tripliveined; domatia only present in the lowermost pair of lateral veins ... 96. *O. vanderwerffii*
82′. Leaves pinnately veined; domatia often present in the axils of more than one pair of lateral veins or along the lateral veins ... 83
83(82). Terminal buds glabrous ... 84
83′. Terminal buds pubescent ... 86
84(83). Leaves broadly elliptic, 17–27 × 8–15 cm ... 29. *O. euvenosa*
84′. Leaves elliptic, 5–18 × 1.5–7 cm ... 85
85(84). Tepals spreading at anthesis; leaves, when dry, yellowish green, the midrib often lighter in color than the laminae ... 100. *O. viridiflora*
85′. Tepals erect or half-erect at anthesis; leaves, when dry, dark green to blackish, the midrib concolorous with the laminae ... 89. *O. tenera*
86(83). Leaf apices obtuse to rounded; leaves coriaceous; domatia conspicuous, restricted to the axils of the lowermost pairs of lateral veins ... 73. *O. pullifolia*
86′. Leaf apices acute; leaves chartaceous to coriaceous; if coriaceous, domatia small and found along the lowermost lateral veins ... 87
87(86). Tertiary venation on lower leaf surface immersed or nearly so; leaves coriaceous to firmly chartaceous, dark green when dry ... 45. *O. jorge-escobarii*
87′. Tertiary venation on lower leaf surface raised; leaves chartaceous, black or yellowish green when dry ... 88
88(87). Inflorescences to 20 cm long; leaves black when dry, the midrib very dark ... 11. *O. bernoulliana*
88′. Inflorescences to 10 cm long; leaves yellowish green when dry, the main veins often lighter in color than the lamina ... 54. *O. meziana*
89(79). Terminal buds glabrous (sometimes a few hairs present along the margins of the bracts surrounding the buds) ... 90
89′. Terminal buds pubescent ... 92
90(89). Flowers and inflorescences glabrous ... 98. *O. verapazensis*
90′. Flowers and distal parts of inflorescences sparsely or moderately, minutely pubescent ... 91
91(90). Leaves 15–35 × 7–15 cm, leaf base rounded, rarely obtuse or subcordate; tepals erect or nearly so at anthesis ... 85. *O. standleyi*
91′. Leaves 10–15 × 4–5 cm, leaf base acute; tepals spreading at anthesis ... 53. *O. matudai*
92(89). Twigs densely pubescent, the surface completely covered by the erect or ascending hairs ... 21. *O. contrerasii*
92′. Twigs glabrous, sparsely pubescent or, if densely pubescent, the hairs appressed ... 93
93(92). Leaves, when dry, yellow-green, rarely darker green; tertiary venation forming a raised reticulum on the lower leaf surface; midrib and lateral veins usually lighter in color than the surrounding leaf tissue ... 94
93′. Leaves, when dry, dark green; tertiary venation not forming a raised reticulum on the lower leaf surface; major veins concolorous with or darker than the leaf tissue ... 95

94(93). Twigs and leaves glabrous or with a few appressed hairs .... 47. *O. laetevirens*

94′. Twigs and major veins on the lower leaf surface moderately pubescent with very short, erect or ascending hairs; indument on the lower leaf surface similar, but sparser .... 78. *O. rovirosae*

95(93). Tepals to 1 mm long and inflorescences moderately to sparsely pubescent, the hairs ascending to erect .... 59. *O. multiflora*

95′. Tepals at least 1.5 mm long; if rarely shorter (1.3–1.5 mm), then inflorescences very sparsely pubescent with appressed hairs 96

96(95). Inflorescences densely pubescent, the surface largely or completely covered by the indument 97

96′. Inflorescences sparsely or moderately pubescent, the surface largely or entirely visible 100

97(96). Leaf apices rounded or obtuse; axillary tufts of hairs lacking on the lower leaf surface .... 19. *O. chrysobalanoides*

97′. Leaf apices acute or acuminate; axillary tufts of hairs present on the lower leaf surface 98

98(97). Leaves obovate, to 4 cm wide, drying green; twigs, when young, alate or sharply angled; lower leaf surface sparsely pubescent, the hairs short, erect and inconspicuous .... 28. *O. eucuneata*

98′. Leaves elliptic or oblanceolate; when widest above the middle, drying black; twigs ridged or angular; lower leaf surface sparsely appressed pubescent or glabrous 99

99(98). Leaves to 2.5 cm wide, oblanceolate or narrowly obovate-elliptic, drying black; tepals ca. 1.5 mm long .... 60. *O. nigrita*

99′. Leaves 2.5–8 cm wide, elliptic or narrowly elliptic-obovate, drying green to dark green; tepals ca. 2 mm long .... 93. *O. uxpanapana*

100(96). Young twigs densely pubescent, the hairs erect; inflorescences 15–20 cm long; domatia lacking .... 88. *O. subalata*

100′. Young twigs appressed pubescent or nearly glabrous; if with some erect hairs, these extremely short and their orientation scarcely visible; inflorescences usually shorter than 15 cm; domatia, as axillary tufts of hairs or shallow pits, often present 101

101(100). Leaves lanceolate; domatia consisting of shallow pits, these with a pubescent or sometimes glabrous margin .... 26. *O. effusa*

101′. Leaves elliptic, ovate or elliptic-obovate; domatia, if present, consisting of axillary tufts of hairs 102

102(101). Leaves 13–25 × 4–8 cm, the tertiary venation raised on the lower surface .... 35. *O. guatemalensis*

102′. Leaves generally smaller than 12 × 5 cm; if occasionally to 15 cm long, the tertiary venation immersed on the lower surface 103

103(102). Leaves elliptic to oblong, the apices rounded or blunt; domatia consisting of tufts of hairs, at least their own diameter away from the midrib .... 39. *O. heribertoi*

103′. Leaves ovate, obovate or elliptic, the apices acute or acuminate; domatia, when present, in the axils of the lateral veins close to the midrib 104

104(103). Leaves ovate, distally tapering into a long and slender apex 105

104′. Leaves broadly or narrowly elliptic, without a long, slender apex 106

105(104). Domatia present as axillary tufts of hairs; outer surface of tepals glabrous .... 63. *O. parvula*

105′. Domatia absent; outer surface of tepals sparsely pubescent .... 87. *O. strigosa*

106(104). Flowers glabrous or nearly so; leaves drying dark green; domatia (as axillary tufts of hairs) visible without magnification .... 75. *O. truncata*

106′. Flowers pubescent, the indument covering the tepals almost completely; leaves drying green to dark green; domatia, when present, not visible without magnification .... 75. *O. racemiflora*

1. Ocotea acuminatissima (Lundell) Rohwer, Bot. Jahrb. Syst. 112: 379. 1991. *Phoebe acuminatissima* Lundell, Contr. Univ. Michigan Herb. 6: 19. 1941. *Cinnamomum acutatum* Kostermans, Reinwardtia 6: 20. 1961, nom. nov. for *Phoebe acuminatissima* Lundell. TYPE: Mexico. Chiapas: *Matuda 2107* (holotype, MICH not seen; isotype, NY!).

Phoebe saxchanalensis Lundell, Contr. Univ. Michigan Herb. 7: 14. 1942. TYPE: Mexico. Chiapas: *Matuda 4311* (holotype, MICH not seen; isotype, MO!).

Phoebe siltepecana Lundell, Wrightia 1: 151. 1946. *Cinnamomum siltepecanum* (Lundell) Kostermans, Reinwardtia 6: 23. 1961. TYPE: Mexico. Chiapas: *Matuda 5140* (holotype, LL not seen).

A variable species characterized by its racemose inflorescences, papillose inner surface of the tepals, spreading tepals at anthesis, and the sparse appressed indument on the lower leaf surface (or leaves almost glabrous).

Distribution. Mexico (Chiapas), Guatemala, from 900 to 2700 m.

2. Ocotea adela van der Werff, Novon 11: 501. 2001. TYPE: Panama. Prov. Panamá: Cerro Jefe, *Croat 13049* (holotype, MO!).

An inconspicuous species best recognized by its unisexual flowers, leaves with slightly impressed lateral veins, and shallow cupules with persistent tepals. It can be confused with the widespread *Ocotea cernua* (Nees) Mez, but that species has often nodding flowers, immersed (not impressed) lateral veins, and does not have persistent tepals on the cupule.

Distribution. Panama, from 500 to 900 m.

3. Ocotea amplifolia (Mez & Donnell Smith) van der Werff, Novon 11: 510. 2001. *Phoebe amplifolia* Mez & Donnell Smith, Bot. Gaz. (Crawfordsville) 19: 261. 1894. *Cinnamomum amplifolium* (Mez & Donnell Smith) Kostermans, Reinwardtia 6: 20. 1961. TYPE: Guatemala. Depto. Quiché: *Heyde & Lux 3033* (syntype, GH!).

Only known from the type collection. The long petioles (3 cm long) and the dense indument on the twigs, inflorescences, and flowers are distinctive.

Distribution. Guatemala, 3000 m.

4. Ocotea arcuata Rohwer, Bot. Jahrb. Syst. 112: 380. 1991. TYPE: Panama. El Llano–Carti Road, *Mori et al. 6883* (holotype, MO!).

A rarely collected species, best recognized by its flowers with spreading tepals with papillose inner surfaces, almost glabrous leaves with pit domatia in the axils of the lowermost lateral veins, and the loop-connected lateral veins.

Distribution. Panama, from 300 to 550 m.

5. Ocotea atirrensis Mez & Donnell Smith, Bot. Jahrb. Syst. 30, Beibl. 67: 18. 1901. TYPE: Costa Rica. *Donnell-Smith 4930* (syntype, US!).

Ocotea paullii C. K. Allen, J. Arnold Arbor. 26: 345. 1945. TYPE: Panama. Coclé: *Allen 1211* (holotype, F not seen; isotype, MO!).
Ocotea pedalifolia Mez, Bot. Jahrb. Syst. 30, Beibl. 67: 19. 1901. TYPE: Costa Rica. Talamanca, *Pittier & Tonduz, in herb. inst. phys.-geogr. Costarica 9172, 9179* (syntypes, BR!).
Ocotea pentagona Mez, Bot. Jahrb. Syst. 30, Beibl. 67: 17. 1901. TYPE: Costa Rica. Rio Naranjo, *Tonduz in herb. inst. phys.-geogr. Costarica 7613* (syntype, BR!); prope San Mateo, *Biolley 7106* (syntype, BR!); without locality, *Tonduz 8362 = Pittier & Durand 8362* (syntype, BR!).
Ocotea wedeliana C. K. Allen, J. Arnold Arbor. 26: 339. 1945. TYPE: Panama. Bocas del Toro: *Cooper 339* (holotype, F not seen; isotype, GH!).

A broad concept of this species is accepted here; distinctive are the hollow twigs, stamens without a sterile tip, and small cupules. For a different viewpoint, see van der Werff (1988a). Only a few *Ocotea* species in Mesoamerica have hollow twigs: *Ocotea jefensis* van der Werff differs in its tomentellous flowers and leaves with decurrent, inrolled bases, while *O. dendrodaphne* Mez has tongue-shaped stamens with a sterile tip and a double-margined cupule.

Distribution. Nicaragua, Costa Rica, and Panama, from 50 to 1200 m.

6. Ocotea atlantica van der Werff, Novon 11: 504. 2001. TYPE: Honduras. Atlántida: *Zamora 1744* (holotype, MO!).

Readily recognized by its small, unisexual flowers and the erect pubescence on the lower leaf surface and twigs; the indument obscures the surface of young twigs.

Distribution. Honduras, Nicaragua, and Costa Rica in forest on the Atlantic slopes from 50 to 400 m.

7. Ocotea aurantiodora (Ruiz & Pavón) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 295. 1889. *Laurus aurantiodora* Ruiz & Pavón, Fl. Peruv. 4, t. 349. 1804. TYPE: Peru. *Ruiz & Pavon s.n.* (B not seen).

Distinctive are the clearly angled twigs, the small, raised reticulation formed by the tertiary venation on the upper leaf surface, and the unisexual flowers. *Ocotea longifolia* HBK, a name widely used for South American specimens, is probably a synonym.

Distribution. Nicaragua, Costa Rica, Panama; much of South America, from 0 to 600 m.

8. Ocotea austinii C. K. Allen, J. Arnold Arbor. 26: 350. 1945. TYPE: Costa Rica. Zarcero, *Austin Smith A 125* (holotype, F not seen; isotype, MO!).

Ocotea irazuensis Lundell, Wrightia 5: 339. 1977. TYPE: Costa Rica. Volcán Irazu, *Proctor 32355* (holotype, LL not seen; isotype, MO!).

Best recognized by the raised reticulation on the upper leaf surface, the inrolled leaf bases, which are decurrent on the petioles, and the coriaceous, frequently oblong leaves.

Distribution. Costa Rica and Panama, from 2000 to 3000 m.

9. Ocotea bajapazensis Lundell, Wrightia 6: 8. 1978. TYPE: Guatemala. *Lundell & Contreras 20946* (holotype, LL not seen; isotypes, F!, MO!).

This species can be recognized by its sparsely appressed pubescent twigs, paniculate-cymose inflorescences, and small flowers (ca. 5 mm diam.). It is similar to *O. heydeana*, which has larger flowers (6.5–9 mm diam.) and occurs at higher altitudes.

Distribution. Guatemala, from 100 to 300 m.

10. Ocotea barbatula Lundell, Wrightia 5: 336. 1977. TYPE: Guatemala. Baja Verapaz: *Lundell & Contreras 19444* (holotype, LL not seen; isotype, MO!).

This species is vegetatively similar to *O. meziana,* but differs in having pit domatia with a pubescent margin and well away from the midrib. More collections may well show that these differences do not hold and that *O. barbatula* is better treated as a synonym of *O. meziana.*

Distribution. Guatemala.

11. Ocotea bernoulliana Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 275. 1889. TYPE: Guatemala. Mujulia, *Bernoulli & Cario 2590* (syntype, U!).

Best recognized by the following combination of characters: twigs, leaves, terminal buds, and flowers glabrous, leaves with conspicuous pit domatia in the axils of lateral veins and smaller pit domatia along the lateral veins, and cupules with 6 prominent longitudinal ridges. This species is rarely collected.

Distribution. Chiapas and Guatemala, from 1000 to 1600 m.

12. Ocotea betazensis (Mez) van der Werff, Novon 9: 572. 1999. *Phoebe betazensis* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 192. 1889. TYPE: Mexico. Oaxaca: *Liebmann 2, 3, 22, 23* (syntypes, C!), *Galeotti 2885* (syntype, not seen), *Jürgensen 575* (syntype, not seen).

Oreodaphne mexicana Meissner var. *diminuta* Meissner, DC. Prodr. 15(1): 118. 1864. *Ocotea mexicana* (Meissner) Hemsley var. *diminuta* (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882. TYPE: Mexico. *Jürgensen 575* (not seen).

Characteristic are the rather broad, elliptic leaves, relatively long (12–23 mm) petioles, filaments half as long as the anthers, and the densely tomentellous or tomentose twigs. This species had been included in *O. helicterifolia,* but that species has frequently obovate leaves, shorter (4–15 mm) petioles, sparse indument on the twigs, and nearly sessile anthers.

Distribution. Oaxaca, to be expected in Chiapas, 2000–2600 m.

13. Ocotea botrantha Rohwer, Bot. Jahrb. Syst. 112(3): 375. 1991, non *Ocotea matudai* Lundell. *Persea matudai* Lundell, Lloydia 4: 49. 1941. TYPE: Mexico. *Matuda 1880* (holotype, MICH not seen; isotype, MO!).

Easily recognized by its racemose inflorescences, large flowers with tongue-shaped stamens, and densely pubescent twigs. It is closely related to *O. sinuata,* which differs in its paniculate-cymose inflorescences and densely pubescent pistils.

Distribution. Chiapas, Guatemala, El Salvador, from 800 to 2400 m.

14. Ocotea bourgeauviana (Mez) van der Werff, Novon 9: 574. 1999. *Phoebe bourgeauviana* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 194. 1889. TYPE: Mexico. Veracruz: *Bourgeau 2234* (syntype, MO!).

Nectandra longicuspis Lundell, Wrightia 5: 34. 1974. TYPE: Guatemala. Izabal: *Contreras 11186* (holotype, LL not seen; isotype, MO!).

Phoebe chinantecorum Schultes, Bot. Mus. Leafl. 9: 170. 1941. *Cinnamomum chinantecorum* (Schultes) Kostermans, Reinwardtia 6: 20. 1961. TYPE: Mexico. Oaxaca: *Schultes & Reko 827* (holotype, GH!).

The combination of clustered leaves and tepals that are glabrous on the outside and pubescent on the inside is diagnostic. It can resemble *O. helicterifolia,* but that species has the inner surface of the tepals glabrous. The two collections from Guatemala and Honduras have the interior of the receptacle pubescent, while the Mexican specimens have a glabrous interior of the receptacle. More collections are needed to determine if the specimens from Guatemala and Honduras are properly placed in *O. bourgeauviana.*

Distribution. Mexico (Veracruz, Oaxaca, Chiapas), Belize, Guatemala, Honduras, from 100 to 1200 m.

15. Ocotea brenesii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 454. 1937. *Nectandra brenesii* (Standley) C. K. Allen, J. Arnold Arbor. 26: 370. 1945. TYPE: Costa Rica. *Brenes 13653* (holotype, F!).

The racemose inflorescences and appressed indument on the young twigs characterize *O. brenesii.* It is similar to *O. pittieri* (Mez) van der Werff, but the latter species has a short, erect indument on the twigs and domatia in the form of axillary tufts of hairs.

Distribution. Costa Rica, Panama, from 700 to 2000 m.

16. Ocotea calophylla Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 298. 1889. *Pleurothyrium velutinum* Meissner, DC. Prodr. 15(1): 170. 1864. TYPE: Colombia. *Jervise s.n.* (holotype, K not seen).

Ocotea fulvescens Standley & Steyermark, Ceiba 1: 237. 1951. TYPE: Costa Rica. Cartago: *Leon 2166* (holotype, F!; isotype, MO!).

A striking species easily recognized by its densely pubescent leaves with a revolute base, the vernation lines on the lower surface, and its upper montane habitat.

Distribution. Costa Rica, northern South America, from 2600 to 3000 m.

17. Ocotea cernua (Nees) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 377. 1889. *Oreodaphne cernua* Nees, Syst. Laurin. 424. 1836. TYPE: Martinique. *Sieber 106* (syntype, MO!).

A common and widely distributed species with nearly glabrous twigs, leaves, inflorescences, and flowers; the unisexual flowers are often somewhat nodding or reflexed. The cupules are deeply cup-shaped; leaves are frequently somewhat tripliveined.

Distribution. From Mexico south to Bolivia and Brazil, from 0 to 700 m.

18. Ocotea chiapensis (Lundell) Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. ser. 23: 114. 1944. *Nectandra chiapensis* Lundell, Contr. Univ. Michigan Herb. 6: 12. 1941. TYPE: Mexico. Chiapas: *Matuda 2042* (holotype, MICH not seen; isotype, MO!).

Distinctive are the leaves with decurrent, inrolled bases, domatia as axillary tufts of hairs, and the relatively large (5–6 mm diam.) flowers. It is similar to *O. glaucosericea* Rohwer from Costa Rica and Panama, but the latter species has a denser indument on leaves and flowers and usually lacks domatia.

Distribution. Mexico (Guerrero, Oaxaca, Chiapas), Guatemala, from 1000 to 2800 m.

19. Ocotea chrysobalanoides (Lundell) Lundell, Wrightia 5: 35. 1974. *Persea chrysobalanoides* Lundell, Wrightia 1: 151. 1946. TYPE: Mexico. Chiapas: *Matuda 5582* (holotype, LL not seen; isotype, MO!).

Only known from the type collection. This species can be recognized by its leaves with obtuse to rounded apices, the pubescent inner surface of the receptacle, large (0.8 mm long) staminodia, and the dense, gray indument on twigs and inflorescences.

Distribution. Mexico (Chiapas), at 2000 m.

20. Ocotea congregata van der Werff, Novon 9: 574. 1999. TYPE: Mexico. Chiapas: *Shilom Ton 8930* (holotype, MO!).

Can be recognized by its loosely clustered leaves, the brown to dark brown indument on the twigs, and the rather long (10 mm or more) petioles. It can be confused with *O. tonii* (Lundell) van der Werff, which differs in its shorter (to 6 mm) petioles and yellowish brown indument on the young twigs.

Distribution. Mexico (Chiapas), from 800 to 1400 m.

21. Ocotea contrerasii Lundell, Wrightia 5: 337. 1977. TYPE: Guatemala. Dept. Baja Verapaz: *Lundell & Contreras 19588* (holotype, LL not seen; isotype, MO!).

A rarely collected species related to *O. meziana*, from which it differs in the dense indument on the twigs, with erect or ascending hairs and spreading hairs along the major veins on the lower leaf surface.

Distribution. Guatemala.

22. Ocotea corrugata van der Werff, Novon 9: 574. 1999. TYPE: Mexico. Oaxaca: *Wendt et al. 6765* (holotype, MEXU not seen; isotype, MO!).

Only known from the type collection and easily recognized by its rugose-bullate, pubescent leaves. Its racemose inflorescences are also a useful character.

Distribution. Mexico (Oaxaca), from 1100 to 1300 m.

23. Ocotea darcyi van der Werff, Novon 11: 505. 2001. TYPE: Panama. *Correa & Montenegro 10176* (holotype, PMA not seen; isotype, MO!).

This species is closely related to *O. stenoneura* Mez & Pittier, which differs in its inrolled and decurrent leaf bases, acute leaf apices, and elliptic leaf shape. It can also be confused with *O. pseudopalmana* Burger, but *O. darcyi* differs in having many-flowered inflorescences, a ferruginous indument (not brown), and smaller flowers (4–4.5 mm vs. 6–8 mm diam.).

Distribution. Panama, from 700 to 1000 m.

24. Ocotea dendrodaphne Mez, Jahrb. Königl. Bot. Gart Berlin 5: 238. 1889. *Dendrodaphne macrophylla* Beurl., Kongl. Vetensk. Acad. Handl. 1854: 145. 1856, non *Ocotea macrophylla* HBK. TYPE: Panama. *Billberg s.n.* (holotype, S not seen).

Ocotea ovandensis Lundell, Contr. Univ. Michigan Herb. 6: 16. 1941. TYPE: Mexico. Chiapas: *Matuda 444* (holotype, MICH not seen).

Ocotea quisara Mez & Donnell Smith, Bot. Gaz. (Crawfordsville) 33: 259. 1902. TYPE: Costa Rica. *J. Donnell Smith 6756* (syntype, BM not seen), *J. Donnell Smith 6751* (syntypes, B, K not seen), *J. Donnell Smith 6753* (syntype, K not seen).

A widespread species, easily recognized by its hollow twigs and tongue-shaped stamens with a sterile tip. The poorly known *O. morae* Gomez-Laurito shares these characters, but has leaves with an inrolled base (flat in *O. dendrodaphne*) and much larger fruits (5 × 3.5 cm vs. 2.5 × 1 cm in *O. dendrodaphne*).

Distribution. From Mexico to Panama, 50–1300 m.

25. Ocotea dentata van der Werff, Fieldiana, Bot., n.s. 23: 79. 1990. TYPE: Costa Rica. *Gomez & Herrera 23653* (holotype, MO!).

Distinctive are the obovate-elliptic leaves with inrolled, decurrent bases and with a rather sparse, erect indument on the lower surface, while the twigs are appressed pubescent.

Distribution. Atlantic slopes of Nicaragua, Costa Rica, and Panama, from 100 to 1000 m.

26. Ocotea effusa (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882. *Oreodaphne effusa* Meissner, DC. Prodr. 15(1): 120. 1864. TYPE: Mexico. Prope S. Pedro Nolasco, Talea etc., *Jürgensen 906* (syntype, BM!).

Best recognized by its lanceolate leaves with shallow, often pubescent pit domatia. The large (0.8 mm) staminodia are also a useful character. Several collections from higher altitude (1700–2000 m) are provisionally placed here.

Distribution. Southern Mexico, Belize, Guatemala, from 200 to 2000 m.

27. Ocotea endresiana Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 257. 1889. TYPE: Costa Rica. *Endres 223* (holotype, K!).

Characterized by its glabrous leaves, inflorescences, and flowers, reflexed leaf bases, and cupules without persistent tepals. Collections from Costa Rica tend to have well-developed domatia, but these are less conspicuous or even lacking in specimens from Panama. Large-leafed specimens resemble *O. rivularis* Standl. & Williams, but that species has puberulous flowers.

Distribution. Costa Rica, Panama, from 200 to 1500 m.

28. Ocotea eucuneata Lundell, Contr. Univ. Michigan Herb. 6: 16. 1941. TYPE: Belize. Stann Creek Distr., *Gentle 3068* (holotype, MICH not seen; isotype, MO!).

Only known from the type collection. Distinguishing features are the obovate leaves with a sparse, erect indument on the lower surface, which is best seen along the major veins, and the sharply angled young twigs.

Distribution. Belize, at 200 m.

29. Ocotea euvenosa Lundell, Wrightia 4: 157. 1971. *Ocotea venosa* Lundell, Phytologia 12: 245. 1965, non Gleason, 1931. TYPE: Guatemala. Alta Verapaz: *Contreras 4678* (holotype, LL!).

Known to me only from the type collection. Diagnostic are the large (to 27 × 15 cm) leaves, drying nearly black, with pinnate venation and pit domatia in the axils of the basal lateral veins. Closely related are *O. bernouilliana*, which has narrower leaves and pit domatia not only in the axils of the basal lateral veins but also along the lateral veins, and *O. vanderwerffii* (Kostermans) van der Werff, which has smaller, tripliveined leaves.

Distribution. Guatemala.

30. Ocotea fendleri (Meissner) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 152. 1986. *Gymnobalanus fendleri* Meissner, DC. Prodr. 15(1): 142. 1864. TYPE: Venezuela. *Fendler 2395* (holotype, G-DC not seen).

Known in Mesoamerica from only two collections, a pistillate and a sterile one; among the species with unisexual flowers best recognized by the dense, shaggy pubescence on the twigs, the decurrent leaf bases, and the erect indument on the lower leaf surface. Identifications of the two Mesoamerican collections are provisional.

Distribution. Panama, Venezuela, French Guyana, at 1000–1100 m.

31. Ocotea floribunda (Swartz) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 325. 1889. *Laurus floribunda* Sw., Prodr. Veg. Ind. Occ., 65. 1788. TYPE: Jamaica. *Swartz s.n.* (holotype, S not seen).

A widespread species, best recognized by its pubescent pistil or pistillode, the rather large (6–7 mm diam.) flowers, and the platelike cupule with a double margin.

Distribution. From Nicaragua south to Brazil and Peru, 100–1400 m.

32. Ocotea glaucosericea Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 144. 1986. *Nectandra hypoglauca* Standl. ex C. K. Allen, J. Arnold Arbor. 26: 399. 1945, non *O. hypoglauca* (Nees) Mez, 1889. TYPE: Panama. Chiriquí: *Davidson 531* (holotype, F not seen; isotype, MO!).

Similar to *O. chiapensis*: see that species for a discussion of the differences.

Distribution. Costa Rica, Panama, from 1500 to 2000 m.

33. Ocotea gomezii Burger, Fieldiana, Bot., n.s., 23: 81. 1990. TYPE: Costa Rica. *Gomez-Laurito et al. 11450* (holotype, CR not seen; isotype, MO!).

A very distinctive species with large (10–14 mm diam.) flowers, densely pubescent twigs, leaves, and flowers, and persistent tepals on the cupule.

Distribution. Costa Rica, possibly Panama, from 800 to 1400 m.

34. Ocotea gordonii van der Werff, Novon 9: 575. 1999. TYPE: Panama. Chiriquí: *McPherson 10421* (holotype, MO!).

This species belongs to the *O. helicterifolia* group and is characterized by its racemose inflorescences, long (ca. 1 cm) pedicels, and its pubescent inner surface of the receptacle. Most other species in this group have paniculate-cymose inflorescences. In Panama only *O. purpurea* (Mez) van der Werff shares the racemose inflorescences, but that species has smaller (5 mm vs. 8–10 mm diam.) flowers.

Distribution. Panama, from 1000 to 1150 m.

35. Ocotea guatemalensis Lundell, Wrightia 5: 339. 1977. TYPE: Guatemala. Baja Verapaz: *Lundell & Contreras 19754* (holotype, LL not seen; isotype, MO!).

A rarely collected species with rather large (to 25 × 8 cm) leaves, conspicuous domatia, and raised reticulation on the lower leaf surface. The density of the pubescence on the inflorescences increases markedly from the base toward the flowers. A few collections from Costa Rica and Panama are provisionally included here; they differ in having smaller (ca. 3 mm vs. 4–5 mm diam.), less pubescent flowers.

Distribution. Guatemala, possibly Costa Rica and Panama.

36. Ocotea haberi van der Werff, Novon 11: 505. 2001. TYPE: Costa Rica. Guanacaste: 4–5 km NW of Monteverde, *Haber, Guindon & Brenes 11093* (holotype, MO!).

An inconspicuous species best recognized by its pubescent flowers, pit or pocket domatia, often with a narrow opening, and a pubescent inner surface of the receptacle. Most other species with pit domatia have glabrous flowers and a glabrous inner surface of the receptacle.

Distribution. Costa Rica, Panama, from 800 to 1400 m.

37. Ocotea hartshorniana Hammel, J. Arnold Arbor. 67: 128. 1986. TYPE: Costa Rica. Heredia: *Hammel 11932* (holotype, DUKE not seen; isotype, MO!).

Best recognized by the erect or ascending hairs on the lower leaf surface, the dense, reddish brown indument on twigs and inflorescences, and the decurrent leaf bases. It is very similar to *O. monteverdensis* Burger, which has a predominantly appressed indument on the lower leaf surface and occurs at higher altitude. It can also be confused with *O. stenoneura,* but that species has inrolled, not flat leaf bases.

Distribution. Costa Rica, Panama, from 100 to 300 m.

38. Ocotea helicterifolia (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882. *Oreodaphne helicterifolia* Meissner, DC. Prodr. 15(1): 123. 1864. *Phoebe helicterifolia* (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 193. 1889. *Cinnamomum helicterifolium* (Meissner) Kostermans, Reinwardtia 6: 21. 1961. TYPE: Mexico. Chiapas: *Linden 1641* (syntype, K!).

Nectandra corzoana Lundell, Wrightia 4: 102. 1969. *Phoebe corzoana* (Lundell) Lundell, Wrightia 5: 342. 1977. *Cinnamomum corzoanum* (Lundell) Kostermans, Reinwardtia 10: 422. 1988. TYPE: Mexico. Chiapas: *Shilom Ton 3560* (holotype, LL!).

Ocotea tenejapensis Lundell, Wrightia 4: 108. 1969. TYPE: Mexico. Chiapas: *Shilom Ton 779* (holotype, LL!).

Oreodaphne mexicana Meissner, DC. Prodr. 15(1): 118. 1864. *Oreodaphne mexicana* var. *subsessilis* Meissner, DC. Prodr. 15(1): 118. 1864, nom. superfl. = var. *mexicana*. *Ocotea mexicana* (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882. *Ocotea mexicana* var. *subsessilis* (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882, nom. superfl. = var. *mexicana*. *Phoebe nectandroides* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 194. 1889, non *Phoebe mexicana* Meissner. TYPE: Mexico. *Galeotti 7004* (lectotype, designated here, BR!), *Jürgensen 537* (syntype, not seen).

Oreodaphne mexicana Meissner var. *longipes* Meissner, DC. Prodr. 15(1): 118. 1864. *Ocotea mexicana* (Meissner) Hemsley var. *longipes* (Meissner) Hemsley, Biol. Centr. Amer., Bot. 3: 73. 1882. TYPE: Mexico. Cerca Orizaba, *Botteri 1018* (syntype, K not seen).

Oreodaphne umbrosa Nees var. *bullata* Meissner, DC. Prodr. 15(1): 122. 1864. *Ocotea umbrosa* var. *bullata* (Nees) Hemsley, Biol. Centr. Amer., Bot. 3: 74. 1882. TYPE: Central America. *Oersted 21* (holotype, B destroyed).

Phoebe obtusata Lundell, Contr. Univ. Michigan Herb. 6: 21. 1941. *Cinnamomum obtusatum* (Lundell) Kostermans, Reinwardtia 6: 22. 1961. TYPE: Mexico. Chiapas: *Matuda 1887* (holotype, MICH not seen; isotype, CAS!).

A widespread and variable species, characterized by the hirsute indument on twigs and leaves, paniculate-cymose inflorescences, glabrous flowers, alternate leaves, and a glabrous inner surface of the receptacle. Collections placed here from Costa Rica have obovate leaves and occur at lower altitudes; they might represent a different species. *Ocotea tenejapensis*, only known from the type, is provisionally included here.

Distribution. From Mexico to Panama, at 1000–1900 m (in Costa Rica at 50–600 m).

39. Ocotea heribertoi Wendt, Lundellia 1: 40. 1998. TYPE: Mexico. Oaxaca: *Wendt et al. 6871* (holotype, MEXU not seen; isotype, MO!).

Tall trees, known from only two collections and best recognized by their smooth leaves with an obtuse or rounded apex, presence of domatia at some distance from the midrib, and its large fruits (to 4.5 cm diam.).

Distribution. Mexico (Oaxaca, to be expected in Chiapas), at 200–300 m.

40. Ocotea heydeana (Mez & Donnell Smith) Bernardi, Candollea 22: 93. 1967. *Nectandra heydeana* Mez & Donnell Smith, Bot. Gaz. (Crawfordsville) 19: 262. 1894. TYPE: Guatemala. *Heyde & Lux 4260* (syntype, MO!).

Can be recognized by its rather large (6.5–9 mm diam.), glabrous flowers, paniculate-cymose inflorescences, and sparsely pubescent twigs. Similar to *O. bajapazensis*, which has smaller (4.5–5.5 mm diam.) flowers and occurs at lower altitudes, and to *O. magnifolia* (Lundell) Lundell, which has a denser indument on the twigs.

Distribution. Guatemala, El Salvador, Honduras, from 600 to 1900 m.

41. Ocotea holdridgeiana Burger, Fieldiana, Bot., n.s. 23: 83. 1990. TYPE: Costa Rica. *Lent 1677* (holotype, F not seen; isotype, MO!).

Easily recognized by the conspicuous pocket domatia in the axils of the basal lateral veins, the large (10 mm diam.) flowers, and the stamens with a sterile tip. Leaves can be somewhat tripliveined.

Distribution. Costa Rica, Panama, from 1600 to 2400 m.

42. Ocotea insularis (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 271. 1889. *Phoebe insularis* Meissner, DC. Prodr. 15(1): 33. 1864. TYPE: Costa Rica. Cocos Island, *Menzies s.n.* (holotype, K not seen; isotype, MO!).

Aiouea lundelliana C. K. Allen, J. Arnold Arbor. 26: 419. 1945. TYPE: Panama. *White 225* (holotype, MO!).

Ocotea ira Mez & Pittier, Bull. Herb. Boiss., Sér. 2, 3: 232. 1903. TYPE: Costa Rica. *Tonduz in Herb. Inst. Phys.-Geogr. Costar. 10415* (syntype, US!), *idem 13399* (syntype, US!).

As accepted here, a variable species with rather large leaves with decurrent bases, small (2.5–3.5 mm diam.) flowers with erect tepals, and tufts of hairs on the back of the inner stamens. Montane populations have often smaller, more coriaceous leaves. Domatia are often, but certainly not always, present.

Distribution. Costa Rica, Panama, Colombia, and Ecuador, from 100 to 2000 m.

43. Ocotea iridescens Lorea-Hernandez & van der Werff, Brittonia 54: 2002 in press. TYPE: Mexico. Oaxaca: Salas.

Among the Mexican species of *Ocotea*, this species is distinctive because of its dense, minute, and light-colored indument on the lower leaf surface, its acuminate leaves, and slender inflorescences. It is known from a few collections made near the border of Oaxaca with Chiapas at 1400–1600 m.

44. Ocotea jefensis van der Werff, Novon 11: 506. 2001. TYPE: Panama. Prov. Panamá: Cerro Jefe, *Carrasquilla 2123* (holotype, MO!).

Diagnostic are the hollow twigs, obovate leaves, and small (4 mm diam.), tomentellous flowers. Its petioles are indistinct due to the decurrent leaf bases.

Distribution. Panama, from 200 to 900 m.

45. Ocotea jorge-escobarii Nelson, Ceiba 25: 173. 1984. TYPE: Honduras. Olancho: *Nelson & Soto 8188* (holotype, TEFH not seen; isotype, MO!).

A montane species with dark green, stiff leaves, pit domatia along the basal lateral veins, and large, ribbed cupules. Closely related is *O. pullifolia* van der Werff, which differs in leaves with obtuse or rounded apices, and in having pit domatia restricted to the axils of the basal lateral veins.

Distribution. Honduras, Nicaragua, from 1000 to 1500 m.

46. Ocotea klepperae van der Werff, Novon 11: 508. 2001. TYPE: Costa Rica. Puntarenas: *Hammel 22068* (holotype, INB not seen; isotype, MO!).

The large flowers, tongue-shaped stamens with a sterile tip, and the position of the inflorescences in axils of bracts near the tips of the branches place this species in the subgenus *Dendrodaphne.* It differs from the other Mesoamerican species of this subgenus in the dense indument on the twigs, inflorescences, and flowers.

Distribution. Costa Rica (2 collections), from 10 to 300 m.

47. Ocotea laetevirens Standley & Steyermark, Field Mus. Publ. Bot. 23: 114. 1944. TYPE: Guatemala. Huehuetenango: Cerro Chiblac, *Steyermark 49378* (holotype, F!).

Ocotea clarkei Lundell, Wrightia 4: 133. 1970. Syn. nov. TYPE: Mexico. Chiapas: *Clarke 38* (holotype, DS!).

As accepted here, a variable species that includes all specimens of the *O. meziana* group with glabrous or sparsely appressed pubescent leaves, pubescent terminal buds, and without domatia or with domatia as axillary tufts of hairs. It is close to *O. meziana,* but that species has pit domatia on the lower leaf surface. Some collections from Costa Rica and Panama that are vegetatively indistinguishable from *O. laetevirens* have 2-celled anthers; in spite of this, they are here included in *O. laetevirens* and not described as new species of *Aiouea* Aubl.

Distribution. Mexico (Chiapas), Guatemala, Honduras, Costa Rica, and Panama, from 100 to 3000 m.

48. Ocotea lentii Burger, Fieldiana, Bot., n.s. 23: 86. 1990. TYPE: Costa Rica. Cartago: *Lent 794* (holotype, F not seen; isotype, MO!).

Distinctive are the large (18–40 cm), obovate leaves, sparsely pubescent leaves, receptacles pubescent on the inner surface and the large (5 × 2.5 cm) fruits. It can be confused with *O. valerioides* Burger, but that species has the twigs and inflorescences completely covered by the indument, while in *O. lentii* part of the surface remains visible. The hairs of *O. lentii* are also coarser.

Distribution. Costa Rica, from 700 to 1400 m.

49. Ocotea leucoxylon (Swartz) Lanessan, Pl. Util. Col. Franc. 156. 1886. *Laurus leucoxylon* Sw., Prodr. Veg. Ind. Occ. 65. 1788. TYPE: Jamaica. *Swartz s.n.* (holotype, S not seen).

Ocotea lenticellata Lundell, Wrightia 5: 54. 1974. TYPE: Guatemala. Izabal: *Contreras 9924* (holotype, LL not seen; isotype, MO!).

Ocotea subsericea Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 456. 1937. TYPE: Costa Rica. *Brenes 6789* (holotype, F!).

Diagnostic are the small, unisexual flowers, leaves with a smooth upper surface, and the minute, appressed, gray indument on the young twigs. The flowers are less densely pubescent than the pedicels. Cupules are shallow to platelike and often lenticellate.

Distribution. From Mexico to Brazil and Peru, West Indies, from 200 to 1600 m.

50. Ocotea macrantha van der Werff, Novon 11: 508. 2001. TYPE: Costa Rica. Puntarenas: Canton de Osa, *Aguilar 4688* (holotype, MO!).

Vegetatively very similar to *O. rubriflora* Mez; both have a short and dense indument on the twigs and inflorescences. However, *O. macrantha* has larger flowers (10–12 mm vs. 6–7 mm diam.).

Distribution. Costa Rica, from 100 to 200 m.

51. Ocotea macropoda (HBK) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 348. 1889. *Persea macropoda* HBK, Nov. Gen. Sp. 2: 127. 1817. TYPE: Colombia. *Humboldt & Bonpland s.n.* (holotype, P not seen).

Ocotea babosa C. K. Allen, Mem. New York Bot. Gard. 15: 82. 1966. Syn. nov. TYPE: Venezuela. *Bernardi 86* (holotype, NY!).

Best recognized by the unisexual flowers and erect indument on twigs, leaves, and flowers. In these characters *O. macropoda* resembles *O. atlantica,* but in the latter species the indument covers the surface of the twigs completely, while it remains partly visible on *O. macropoda. Ocotea macropoda* also has larger flowers than *O. atlantica* (5–6 mm vs. 3.5 mm diam.). I am not quite certain that the name *O. macropoda* is correctly applied here; the South American specimens (including the types of *O. macropoda* and *O. babosa*) come from much higher altitude (above 2000 m).

Distribution. Costa Rica, Panama, Colombia, Venezuela, Ecuador, from 100 to 800 m.

52. Ocotea magnifolia (Lundell) Lundell, Wrightia 5: 341. 1977. *Nectandra magnifolia* Lundell, Wrightia 4: 103. 1969. TYPE: Guatemala. Alta Verapaz: *Contreras 7865* (holotype, LL not seen; isotype, MO!).

Nectandra thornei Lundell, Wrightia 5: 335. 1977. Syn. nov. TYPE: Mexico. Chiapas: *Thorne & Lathrop 40526* (holotype, LL not seen; isotype, DS!).

A poorly known and poorly defined species, best recognized by its indument, which is denser than in *O. heydeana* and sparser than in *O. rubriflora* Mez.

Distribution. Mexico (Chiapas), Guatemala, from 100 to 200 m.

53. Ocotea matudai Lundell, Bull. Torrey Bot. Club 69: 388. 1942. TYPE: Mexico. Chiapas: Mt. Ovando, *Matuda 4221* (holotype, MICH not seen; isotype, F!).

A rarely collected species best recognized by its glabrous terminal buds and leaves; flowers have spreading tepals at anthesis. The distal parts of the inflorescences have a minute, predominantly erect indument, also a useful character.

Distribution. Mexico (Chiapas), 1300–2700 m.

54. Ocotea meziana C. K. Allen, J. Arnold Arbor. 26: 360. 1945. TYPE: Costa Rica. Zarcero, *Austin Smith H359* (holotype, F not seen; isotype, MO!).

A rather common species, characterized by its greenish drying leaves with small pit domatia along the lateral veins, pubescent terminal buds, and glabrous flowers. It is similar to *O. viridiflora* Lundell, which differs in its glabrous terminal buds, finely acute leaf apices, and smaller inflorescences (to 5 cm in *O. viridiflora*, to 10 cm in *O. meziana*). Also similar to *O. laetevirens*, but this species lacks pit domatia.

Distribution. Honduras, Nicaragua, Costa Rica, and Panama, from 100 to 1800 m.

55. Ocotea mollicella (Blake) van der Werff, Fieldiana, Bot., n.s. 23: 88. 1990. *Phoebe mollicella* Blake, Contr. Gray Herb. 52: 64. 1917. *Cinnamomum mollicellum* (Blake) Kostermans, Reinwardtia 6: 22. 1961. TYPE: Costa Rica. Copey, *Tonduz 11676* (holotype, GH!).

Readily recognized by its racemose inflorescences, elliptic to narrowly elliptic leaves with soft, gray pubescence, and the densely pubescent twigs. It is infrequently collected.

Distribution. Costa Rica, from 1400 to 2300 m.

56. Ocotea mollifolia Mez & Pittier, Bull. Herb. Boissier, ser. 2, 3: 233. 1903. TYPE: Costa Rica. *Pittier 16031* (holotype, B not seen).

Best recognized by its densely pubescent twigs, pubescent, chartaceous leaves, and many-flowered inflorescences. See also under *O. darcyi* and *O. pseudopalmana* Burger.

Distribution. Costa Rica, Panama, from 50 to 1000 m.

57. Ocotea monteverdensis Burger, Fieldiana, Bot., n.s. 23: 89. 1990. TYPE: Costa Rica. Puntarenas: *Hartshorn 1900* (holotype, CR not seen; isotype, MO!).

Similar to *O. hartshorniana*; see that species for differences.

Distribution. Costa Rica, from 800 to 1500 m.

58. Ocotea morae Gomez-Laurito, Novon 7: 145. 1997. TYPE: Costa Rica. Alajuela: *Gomez-Laurito & Mora 12817* (holotype, USJ not seen; isotype, MO!).

The tongue-shaped stamens and double-margined cupule place this species in subgenus *Dendrodaphne*. It can be confused with the widespread *O. dendrodaphne*, but differs in its inrolled leaf base and large (5 × 3.5 cm) fruits.

Distribution. Costa Rica, from 100 to 800 m.

59. Ocotea multiflora van der Werff, Novon 6: 481. 1996. TYPE: Costa Rica. Puntarenas: Reserva Forestal Golfo Dulce, *Aguilar 791* (holotype, MO!).

Tall trees, best recognized by its leaves with many (12 to 17) pairs of lateral veins, the many-flowered inflorescences, and small (2–2.5 mm diam.) flowers. It was included in Burger and van der Werff (1990) as *Ocotea sp. B.*

Distribution. Only known from the Osa Peninsula in Costa Rica, from 10 to 200 m.

60. Ocotea nigrita (Lundell) Lundell, Wrightia 5: 341. 1977. *Nectandra nigrita* Lundell, Wrightia 4: 132. 1970. TYPE: Guatemala. El Petén: *Contreras 9465* (holotype, LL not seen; isotype, CAS!).

An infrequently collected species, characterized by its oblanceolate, black-drying leaves with tufts

of hairs in the axils of the basal lateral veins and the small (3–4 mm diam.), densely puberulous flowers. This species can be confused with *O. uxpanapana* Wendt & van der Werff, which differs in its longer and wider leaves (6–15 × 1.5–2.5 cm in *O. nigrita*, 10–25 × 2.5–8 cm in *O. uxpanapana*) and larger (3–4 mm vs. 4–6 mm diam.) flowers.

Distribution. Guatemala, from 200 to 300 m.

61. Ocotea oblonga (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 367. 1889. *Mespilodaphne oblonga* Meissner, DC. Prodr. 15(1): 107. 1864. TYPE: French Guyana, *Sagot 491* (holotype, G-DC not seen).

Phoebe mayana Lundell, Amer. Midl. Naturalist 29: 473. 1943. *Ocotea mayana* (Lundell) Lundell, Wrightia 2: 52. 1960. *Cinnamomum mayanum* (Lundell) Kostermans, Reinwardtia 10: 446. 1988. TYPE: Belize. *Gentle 3187* (holotype, MICH not seen; isotype, MO!).

This species can be easily recognized by the combination of unisexual flowers and leaves with pit or slit domatia. The slender, appressed pubescent vegetative buds are also a good character.

Distribution. From Mexico to Bolivia and Brazil, from 0 to 1000 m.

62. Ocotea oblongifolia van der Werff, Novon 11: 509. 2001. TYPE: Guatemala. Quezaltenango: Finca St. John, ca. 5 km S of Sta. Maria de Jesus, *Walker 442* (holotype, US!).

Diagnostic are the oblong, densely pubescent leaves with an obtuse to subcordate base and the small (2–3 mm diam.) flowers. The indument is similar to what is found in the *O. helicterifolia* group, but the small flowers with erect to half-erect tepals are entirely different.

Distribution. Only known from the type collection, Guatemala, 1400–1800 m.

63. Ocotea parvula (Lundell) van der Werff, Novon 11: 510. 2001. *Phoebe parvula* Lundell, Wrightia 5: 343. 1977. *Cinnamomum parvulum* (Lundell) Kostermans, Reinwardtia 10: 448. 1988. TYPE: Mexico. Chiapas: *Ton 605* (holotype, LL!).

An infrequently collected species with ovate leaves, gradually tapering into the tip, domatia as axillary tufts of hairs, glabrous tepals, and small (to 5 cm long) inflorescences with frequently persisting bracts. See also *O. strigosa* van der Werff.

Distribution. Mexico (Chiapas, Oaxaca), from 1800 to 2800 m.

64. Ocotea patula van der Werff, Novon 9: 577. 1999. TYPE: Costa Rica. Puntarenas: *Aguilar et al. 2715* (holotype, MO!).

Part of the *O. helicterifolia* group and similar to *O. valeriana* (Standl.) Burger, from which it differs in its densely tomentellous inflorescences (with the surface almost entirely or entirely covered), its shorter (2–3 mm vs. 6–8 mm) pedicels, and its pubescent flowers.

Distribution. Known from two collections, Costa Rica, 1000–1400 m.

65. Ocotea pausiaca Rohwer, Bot. Jahrb. Syst. 112: 387. 1991. TYPE: Panama. Colón: *Knapp 5782* (holotype, MO!).

Part of the *O. heydeana* group, characterized by rather large, glabrous or nearly glabrous flowers with spreading tepals, these with some papillae on the inner surface, and often dark-drying leaves. It is distinct within this group by its stamens with the filaments twice as long as the anthers and the outer six stamens curved inward. Vegetatively it is like *O. rubriflora*, which differs in the very dense, minute indument on the young twigs.

Distribution. Panama, from 900 to 1500 m.

66. Ocotea pharomachrosorum Gomez-Laurito, Novon 3: 31 1993. TYPE: Costa Rica. San José: *Gomez-Laurito et al. 12160* (holotype, CR not seen; isotype, MO!).

A very distinctive species characterized by its stamens with a sterile tip and the densely tomentellous whitish lower leaf surfaces. It was included in Burger and van der Werff (1990) as "A species of uncertain generic position" and in Rohwer (1991) as *Ocotea sp. A.*

Distribution. Costa Rica, Panama, from 1800 to 2200 m.

67. Ocotea pittieri (Mez) van der Werff, Fieldiana, Bot., n.s. 23: 92. 1990. *Phoebe pittieri* Mez, Bot. Jahrb. Syst. 30, Beibl. 67: 16. 1901. *Cinnamomum pittieri* (Mez) Kostermans, Reinwardtia 6: 23. 1961. TYPE: Costa Rica. Alajuela: *Tonduz 11893* (holotype, B not seen).

Best recognized by its racemose inflorescences and the dense, short, erect indument on the young twigs. The indument on the lower leaf surface can be very sparse and difficult to see. *Ocotea pittieri* is very similar to *O. brenesii*, which has appressed hairs on the twigs. The name *O. pittieri* was applied in Burger and van der Werff (1990) to the species here treated as *O. praetermissa* van der Werff.

Distribution. Costa Rica, from 1800 to 2200 m.

68. Ocotea platyphylla (Lundell) Rohwer, Bot. Jahrb. Syst. 112: 390. 1991. *Phoebe platyphylla* Lundell, Contr. Univ. Michigan Herb. 6: 23. 1941. *Nectandra platyphylla* (Lundell) C. K. Allen, J. Arnold Arbor. 26: 402. 1945. TYPE: Mexico. Chiapas: *Matuda 1930* (holotype, MICH not seen; isotype, MO!).

Very similar to *O. heydeana,* from which it differs in its narrowly inrolled or revolute leaf bases.

Distribution. Mexico (Chiapas), Guatemala, El Salvador, from 900 to 2600 m.

69. Ocotea praetermissa van der Werff, Novon 6: 482. 1996. TYPE: Costa Rica. Cartago: *Burger et al. 12065* (holotype, MO!).

Similar to *O. purpurea,* but *O. praetermissa* can be recognized by its paniculate-cymose (not racemose) inflorescences and its glabrous (not pubescent) flowers.

Distribution. Costa Rica, Panama, from 2000 to 3200 m.

70. Ocotea producta (C. K. Allen) Rohwer, Mitt. Inst. Allg. Bot. Hamburg 20: 143. 1986. *Nectandra producta* C. K. Allen, J. Arnold Arbor. 26: 352. 1945. TYPE: Costa Rica. Prov. San José: *Skutch 3906* (holotype, GH not seen; isotype, MO!).

Only known from the type collection and characterized by the long (4–5 cm) apparent petioles with inrolled, decurrent leaf bases. The filaments of the inner 3 stamens are fused.

Distribution. Costa Rica, 700 m.

71. Ocotea pseudopalmana Burger, Fieldiana, Bot., n.s. 23: 92. 1990. TYPE: Costa Rica. San José: *Lent 1679* (holotype, F!).

Diagnostic are the coriaceous leaves with erect indument on the lower surface, the few-flowered inflorescences, the large (6–8 mm diam.) flowers, and the montane habitat. It can be confused with *O. mollifolia,* which has chartaceous leaves, smaller (3–6 mm diam.) flowers, and occurs usually below 1000 m.

Distribution. Costa Rica, Panama, from 2200 to 2900 m.

72. Ocotea puberula (Richard) Nees, Syst. Laurin. 472. 1836. *Laurus puberula* Richard, Actes Soc. Hist. Nat. Paris 1: 108. 1792. TYPE: French Guyana. *Le Blond s.n.* (holotype, P not seen).

Ocotea pyramidata Blake ex Brandegee, Univ. Calif. Publ. Bot. 7: 326. 1920. TYPE: Mexico. Veracruz: *Purpus 8456* (holotype, US not seen; isotype, MO!).

A widespread species, best recognized by its unisexual flowers, the slightly raised reticulation on the upper leaf surface, and the rather large, (thinly) chartaceous leaves. *Ocotea leucoxylon* has the upper surface of the leaves generally smooth and smaller (3–4 vs. 4–5 mm diam.) flowers.

Distribution. From Mexico to Argentina (in Mesoamerica known from Chiapas, Costa Rica, and Panama), from 0 to 1300 m.

73. Ocotea pullifolia van der Werff, Novon 11: 509. 2001. TYPE: Costa Rica. Puntarenas: Canton de Golfito, *Herrera 4119* (holotype, INB!).

Closely related to *O. jorge-escobarii* from Honduras and Nicaragua. *Ocotea pullifolia* is best recognized by its obtuse or rounded leaf apices and in having pit domatia restricted to the axils of the lowermost lateral veins. In some Panamanian collections the pit domatia are lacking.

Distribution. Costa Rica, Panama, from 200 to 1100 m.

74. Ocotea purpurea (Mez) van der Werff, Novon 9: 579. 1999. *Phoebe purpurea* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 196. 1889. TYPE: Guatemala. Alta Verapaz: *von Tuerckheim 371* (syntypes, B, K, LE not seen, photo MO!).

Nectandra capituliforma Lundell, Wrightia 5: 33. 1974. TYPE: Guatemala. *Contreras 11235* (holotype, LL not seen; isotype, MO!).

Readily identified by its usually racemose inflorescences, rather small (to 11 cm long) leaves, and sparsely pubescent flowers. Specimens from Panama differ in having fewer lateral veins (mostly 4 pairs).

Distribution. Mexico (Oaxaca, Chiapas), Guatemala, Honduras, Panama, from 1400 to 2600 m.

75. Ocotea racemiflora Lundell, Wrightia 4: 107. 1969. TYPE: Guatemala. Alta Verapaz: *Contreras* 7904 (holotype, LL!).

Only known from the type collection, which is in fruit with a few detached, old flowers. The flat, thin cupules with persistent tepals and roundish fruits are not known from other Mesoamerican species.

Distribution. Guatemala.

76. Ocotea rhytidotricha Rohwer, Bot. Jahrb. Syst. 112: 391. 1991. TYPE: Nicaragua. Matagalpa: *Hall & Bockus 7919* (holotype, MO!).

Part of the *O. heydeana* group and characterized by the short, erect indument on the lower leaf surface. The hairs are inconspicuous, not discernable to the touch, and are best seen along the major veins.

Distribution. El Salvador, Honduras, Nicaragua, from 1200 to 1600 m.

77. Ocotea rivularis Standley & L. O. Williams, Ceiba 1: 238. 1951. TYPE: Costa Rica. Puntarenas: *Allen 5590* (holotype, EAP not seen; isotype, MO!).

Readily recognized by its large (30–50 cm long), obovate leaves and pubescent flowers. It can be confused with *O. endresiana*, which has smaller (10–30 cm long) leaves and glabrous flowers.

Distribution. Costa Rica, from 50 to 300 m.

78. Ocotea rovirosae Lorea-Hernandez & van der Werff, Brittonia 54: 2002 in press. TYPE: Mexico. Veracruz.

This species is best recognized by the combination of its short, erect indument on twigs and leaves, the paniculate-cymose, many-flowered inflorescences, and the rather large (14–35 cm long), yellowish green drying leaves. *Nectandra lundellii* C. K. Allen, known from the same area, has similarly large, yellow-green drying leaves, but has typical *Nectandra* flowers with the inner surface of the tepals and the stamens papillose; its tepals are also spreading (not erect or half-erect) at anthesis.

Distribution. Mexico (Oaxaca, Tabasco, Veracruz), from 10 to 200 m.

79. Ocotea rubriflora Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 279. 1889. *Nectandra rubriflora* (Mez) C. K. Allen, J. Arnold Arbor. 26: 372. 1945. TYPE: Mexico. Tabasco: *Linden s.n.* (syntype, G!).

Ocotea perseifolia Mez & Donnell Smith, Bot. Gaz. (Crawfordsville) 20: 10. 1895. TYPE: Guatemala. Izabal: *J. Donnell Smith 1807* (syntypes, B not seen, US not seen).

This belongs to the *O. heydeana* group in which it stands apart by the dense and minute indument on the twigs and inflorescences, which covers the surface completely. Vegetatively close to *O. macrantha*, but that species has larger flowers (10–12 vs. 6–7 mm diam.).

Distribution. From southern Mexico to Panama, at 100–350 m.

80. Ocotea rubrinervis Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 351. 1889. TYPE: Peru. *Spruce 4580* (syntype, B!); Panama. *Duchassaing s.n.* (syntype, not seen).

In Mesoamerica only known from the Pacific coast of Panama and best recognized by its unisexual flowers, the readily visible gland dots on the upper leaf surface, and the shallow cupules with persistent tepals.

Distribution. Panama, from 0 to 50 m.

81. Ocotea rufescens van der Werff, Novon 6: 479. 1996. TYPE: Costa Rica. Limón: *Aguilar & Schmidt 1077* (holotype, MO!).

The only *Ocotea* species in Costa Rica and Panama (where it is expected to grow as well) with a dense, reddish brown or reddish indument on twigs and lower leaf surface. *Ocotea salvinii* Mez, from Mexico and Guatemala, has a similar indument but has inrolled leaf bases.

Distribution. Costa Rica, from 450 to 1500 m.

82. Ocotea salvadorensis (Lundell) van der Werff, Novon 6: 481. 1996. *Nectandra salvadorensis* Lundell, Wrightia 4: 105. 1969. *Phoebe salvadorensis* (Lundell) Lundell, Wrightia 5: 344. 1977. TYPE: El Salvador. *P. H. Allen 7173* (holotype, LL not seen; isotype, GH!).

Only known from the type collection. The dense, tomentellous, gray-brown indument on the lower leaf surface is diagnostic. Such an indument also occurs in *O. pharomachosorum*, which has tongue-shaped stamens with a sterile tip, and *O. iridescens*, which has domatia. A few collections from montane cloud forest in Honduras will key to *O. salvadorensis*, but differ from that species in their reddish brown indument on twigs and leaves, and the rather dense indument on the inner surface of the tepals. More collections are needed to determine if the specimens from Honduras represent an undescribed species.

Distribution. El Salvador, at 2500 m.

83. Ocotea salvinii Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 264. 1889. *Phoebe salvinii* (Mez) Lundell, Contr. Univ. Michigan Herb. 6: 23. 1941. *Cinnamomum salvinii* (Mez) Kostermans, Reinwardtia 6: 23. 1961. TYPE: Guatemala. *Salvin s.n.* (syntypes, K not seen, W not seen).

Diagnostic are the ferruginous tomentellous leaves with an inrolled base and the perfect flowers. See also under *O. rufescens.*

Distribution. Chiapas and Guatemala, from 2400 to 3000 m.

84. Ocotea sinuata (Mez) Rohwer, Bot. Jahrb. Syst. 112(3): 373. 1991. *Nectandra sinuata* Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 402 (1889). TYPE: Guatemala. *Bernoulli & Cario 2581* (syntypes, B, GOET, K, LE all not seen).

Best recognized by its large (13–16 mm diam.) flowers, anthers with a sterile tip and densely brown-tomentose twigs. It can be confused with *O. botrantha*; see that species for differences.

Distribution. From southern Mexico to Panama, but not reported from Honduras and Nicaragua, from 200 to 1500 m.

85. Ocotea standleyi C. K. Allen, J. Arnold Arbor. 26: 343. 1945. *Phoebe macrophylla* Standley & Steyermark, Field Mus. Publ. Bot. 23: 116. 1944, non *Phoebe macrophylla* (Blume) Blume. 1851. TYPE: Guatemala. Alta Verapaz: *Standley 70009* (holotype, F not seen).

Readily recognized by its large (15–35 cm long) leaves with a rounded to subcordate base, and the glabrous terminal buds and leaves. A *Licaria* species occurring in Chiapas is vegetatively similar, but its flowers (with only 3 stamens) and cupule (deeply cup-shaped with a weakly developed double margin) set it apart. The *Licaria* species generally occurs below 1000 m.

Distribution. Mexico (Chiapas), Guatemala, from 800 to 2500 m, mostly above 1500 m.

86. Ocotea stenoneura Mez & Pittier, Bull. Herb. Boissier, ser. 2, 3: 233. 1903. TYPE: Costa Rica. San Jose de Dota, *Tonduz 13377* (lectotype, designated by Allen (1945: 334), GH not seen; isolectotype, US!).

A rarely collected species with decurrent, revolute leaf bases, an erect, rather dense indument on the lower leaf surface, and prominently raised venation on the lower leaf surface. Specimens placed here vary in cupule shape, and more collections are needed to determine if two species are involved.

Distribution. Costa Rica, Panama, possibly Colombia and Ecuador, from 700 to 1700 m.

87. Ocotea strigosa van der Werff, Ann. Missouri Bot. Gard. 75: 723. 1988. TYPE: Nicaragua. Matagalpa: *Stevens 22181* (holotype, MO!).

An inconspicuous species with ovate leaves and few-flowered inflorescences. It is similar to *O. parvula*, but that species has domatia and glabrous (not sparsely pubescent) flowers. *Ocotea iridescens* is also a close relative, but differs in its dense indument on the lower leaf surface.

Distribution. Nicaragua, from 1000 to 1600 m.

88. Ocotea subalata Lundell, Lloydia 4: 48. 1941. TYPE: Mexico. Chiapas: *Matuda 2957* (holotype, MICH not seen; isotype, F!).

Only known from two collections. Useful characters for identification are the long (to 20 cm) inflorescences and the sharply angled or winged, densely pubescent young twigs.

Distribution. Mexico (Chiapas), from 2100 to 2500 m.

89. Ocotea tenera Mez & Donnell Smith, Bull. Herb. Boissier, ser. 2, 3: 234. 1903. TYPE: Costa Rica. *Pittier 13396* (syntype, US!).

Ocotea effusoides Lundell, Wrightia 6: 9. 1978. Syn. nov. TYPE: Guatemala. *Lundell & Contreras 20948* (holotype, LL not seen; isotype, MO!).

Ocotea eucymosa Lundell, Wrightia 5: 35. 1974. Syn. nov. TYPE: Guatemala. *Contreras 11215* (holotype, LL not seen; isotype, MO!).

This species is best recognized by its small size (to 12 m tall), dark-drying leaves with gland dots on the upper leaf surface, glabrous terminal buds, and small, glabrous flowers with erect or half-erect tepals.

Distribution. Guatemala and Costa Rica, from 100 to 1600 m.

90. Ocotea tonduzii Standley, Field Mus. Publ. Bot. 18: 456. 1937. *Ocotea cuneata* Mez, Bot. Jahrb. 30, Beiblatt 67: 17. 1901, non *Ocotea cuneata* (Grisebach) Gomez, 1889. TYPE: Costa Rica. *Tonduz 2142* (syntype, BR!).

Characteristic are the dense, reddish indument on the flowers, the large, glabrous (or finely appressed pubescent) terminal buds, the raised tertiary venation on the lower leaf surface, and the glabrous, nearly sessile leaves with an inrolled base. *Ocotea endresiana* has a similar appearance but lacks the reddish indument of the flowers.

Distribution. Costa Rica, from 1500 to 2400 m.

91. Ocotea tonii (Lundell) van der Werff, Novon 9: 579. 1999. *Nectandra tonii* Lundell, Wrightia 4: 106. 1969. TYPE: Mexico. Chiapas: *Shilom Ton 2014* (holotype, LL not seen; isotype, NY!).

Distinctive are the clustered leaves with short (to 6 mm long) petioles, yellow-brown indument, pa-

niculate-cymose inflorescences, and pubescent flowers. See also under *O. congregata.*

Distribution. Mexico (Chiapas), from 1000 to 1500 m.

92. Ocotea truncata Lundell, Phytologia 12: 244. 1965. TYPE: Guatemala. Alta Verapaz: *Contreras 4731* (holotype, LL not seen; isotype, US!).

This species can be recognized by its thin, dark green drying leaves with rather conspicuous domatia and its few-flowered inflorescences with glabrous flowers. The truncate apex of the young fruits is less pronounced in mature fruits and scarcely helps in the identification of this species.

Distribution. Mexico (Chiapas), Guatemala, from 700 to 1200 m.

93. Ocotea uxpanapana Wendt & van der Werff, Ann. Missouri Bot. Gard. 74: 413. 1987. TYPE: Mexico. Veracruz: Mpio. Minatitlán, *Wendt et al. 2869* (holotype, MEXU not seen; isotype, MO!).

Currently only known from the Uxpanapa region in Veracruz. It resembles *O. eucuneata* and *O. nigrita* but differs in its rather large (to 25 cm long), elliptic leaves and slightly larger flowers. The strongly lobed cupules appear to be a unique feature of this species, but cupules of *O. eucuneata* and *O. nigrita* are not yet known.

Distribution. Mexico (Veracruz), to be expected in Chiapas, from 100 to 300 m.

94. Ocotea valeriana (Standley) Burger, Fieldiana, Bot., n.s. 23: 96. 1990. *Phoebe valeriana* Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 18: 460. 1937. *Cinnamomum valerianum* (Standley) Kostermans, Reinwardtia 6: 24. 1961. TYPE: Costa Rica. *Tonduz 11746* (holotype, F not seen).

Nectandra austinii C. K. Allen, J. Arnold Arbor. 26: 374. 1945. TYPE: Costa Rica. Alajuela: *Austin Smith P 2226* (holotype, A not seen).

Phoebe smithii C. K. Allen, J. Arnold Arbor. 26: 317. 1945. *Cinnamomum smithianum* Kostermans, Reinwardtia 6: 23. 1961, non *Cinnamomum smithii* Lukmanoff. TYPE: Costa Rica. Alajuela: *Austin Smith P.C. 307* (holotype, F not seen).

Similar to *O. helicterifolia,* from which it differs in its indument of the twigs (short matted hairs and longer, erect ones in *O. valeriana* vs. only long, erect ones in *O. helicterifolia*), its deeper cupules, and its presence at higher altitudes.

Distribution. Costa Rica and Panama, from 800 to 2200 m.

95. Ocotea valerioides Burger, Fieldiana, Bot., n.s. 23: 97. 1990. TYPE: Costa Rica. *Hartshorn 1530* (holotype, CR not seen; isotype, MO!).

Distinctive are the large (to 40 cm long) leaves and the dense, tomentellous indument on the twigs and inflorescences. Differences with *O. lentii* are discussed under that species.

Distribution. Costa Rica, Panama, from 50 to 500 m.

96. Ocotea vanderwerffii (Kostermans) van der Werff, Novon 11: 511. 2001. *Phoebe glabra* van der Werff, Ann. Missouri Bot. Gard. 74: 406. 1987, non *Ocotea glabra* van der Werff. *Cinnamomum vanderwerffii* Kostermans, Reinwardtia 10: 454. 1988, non *Cinnamomum glabrum* Ettinghausen. TYPE: Mexico. Oaxaca: *Wendt et al. 4813* (holotype, MO!).

Ocotea vanderwerffii is best recognized by its dark-drying, tripliveined leaves with large pit domatia in the axils of the basal lateral veins and the glabrous flowers with erect tepals. It resembles *O. tenera,* but that species has pinnately veined leaves and small pit domatia, which are not visible on the upper surface.

Distribution. Southern Mexico from 150 to 1200 m.

97. Ocotea veraguensis (Meissner) Mez, Jahrb. Königl. Bot. Gart. Berlin 5: 240. 1889. *Sassafridium veraguensis* Meissner, DC. Prodr. 15(1): 171. 1864. TYPE: Costa Rica. *Bridges s.n.* (syntype, K not seen), *Oersted, Laur. 10* (syntype, B not seen), *Warszewicz 1* (syntype, G not seen).

Ocotea bakeri Blake, Contr. Gray Herb. 52: 65. 1917. TYPE: Nicaragua. *Baker 2493* (holotype, GH not seen).

Ocotea escuintlensis Lundell, Contr. Univ. Michigan Herb. 6: 15. 1941. TYPE: Mexico. Chiapas: *Matuda 654* (holotype, MICH not seen).

Ocotea paradoxa Mez, Bot. Jahrb. 30, Beibl. 67: 16. 1901. TYPE: Costa Rica. *Tonduz in Herb. Inst. Phys.-Geogr. Costar. 7648* (holotype, BR!).

A widespread and rather frequently collected species, best recognized by its papillose, tongue-shaped stamens with a sterile tip, solid stems, glabrous (or nearly so) leaves, and its cupules with a double margin. Can be confused with *O. dendro-*

daphne, which has hollow twigs and a pubescent inside of the receptacle.

Distribution. From southern Mexico to Panama, from 10 to 2000 m.

98. Ocotea verapazensis Standley & Steyermark, Field Mus. Publ. Bot. 23: 114. 1944. TYPE: Guatemala. *Standley 71421* (holotype, F!).

A poorly known species with glabrous terminal buds, twigs, and leaves, and slightly winged petioles. Vegetatively similar to *O. subalata,* but that species has densely pubescent terminal buds and pubescent inflorescences and flowers.

Distribution. Guatemala, from 1500 to 2000 m.

99. Ocotea verticillata Rohwer, Bot. Jahrb. Syst. 112(3): 369. 1991. TYPE: Mexico. Veracruz: *Ibarra 2328* (holotype, MO!).

Characteristic are the whorled leaves abruptly rounded at the base and its tongue-shaped stamens with a sterile tip. Related to *O. botrantha* and *O. sinuata,* both of which have alternate leaves.

Distribution. Mexico (Veracruz, Oaxaca), from 100 to 1000 m.

100. Ocotea viridiflora Lundell, Wrightia 5: 36. 1974. TYPE: Panama. Chiriquí: *Proctor 31916* (holotype, LL not seen; isotype, MO!).

Similar to *O. meziana,* but differing in its glabrous terminal buds and sharply acute leaf apices. Collections from Panama have persistent tepals on the cupule; those from Costa Rica do not.

Distribution. Costa Rica, Panama, from 1300 to 1800 m.

101. Ocotea whitei Woodson, Ann. Missouri Bot. Gard. 24: 188. 1937. *Nectandra whitei* (Woodson) C. K. Allen, J. Arnold Arbor. 26: 398. 1945. TYPE: Panama. Chiriquí: *Seibert 307* (holotype, MO!).

Ocotea eusericea Lundell, Wrightia 5: 338. 1977. TYPE: Panama. Chiriquí: *Proctor 31858* (holotype, LL not seen; isotype, MO!).

Ocotea skutchii C. K. Allen, J. Arnold Arbor. 26: 352. 1952. TYPE: Costa Rica. *Skutch 3062* (holotype, GH not seen; isotype, MO!).

As accepted here, a variable species best recognized by the dorsally pubescent filaments of the inner 3 stamens, the rather narrow (2–5 cm wide), frequently oblanceolate or obovate-elliptic leaves with a decurrent and sometimes slightly inrolled base.

Distribution. Nicaragua, Costa Rica, and Panama, from 100 to 2500 m.

Imperfectly Known Species

102. Ocotea sp. A.

Resembles *O. brenesii,* from which it differs in its cymose-paniculate (not racemose) inflorescence, a denser indument of the the twigs, and a glabrous (not pubescent) inner surface of the receptacle. It is only known from one collection, *Carvajal 328* (MO), from Costa Rica. It is likely an undescribed species, but more material is needed for a description. In Rohwer (1991) it was included as *Ocotea sp. B.*

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PHYLOGENETIC RELATIONSHIPS IN EUPHORBIEAE (EUPHORBIACEAE) BASED ON ITS AND *ndh*F SEQUENCE DATA[1]

Victor W. Steinmann[2,3] *and J. Mark Porter*[2]

Abstract

The monophyly and phylogenetic relationships of the tribe Euphorbieae (Euphorbiaceae) were evaluated using separate weighted maximum parsimony analyses of nucleotide sequences of the nrDNA internal transcribed spacer (ITS) region and cpDNA coding region *ndh*F. The study included 223 ingroup species representing nearly all of the previously recognized genera, subgenera, and sections within the Euphorbieae and 4 outgroup taxa from the tribe Hippomaneae (Euphorbiaceae). Both the ITS and *ndh*F analyses support the monophyly of Euphorbieae in addition to the monophyly of its three subtribes, Anthosteminae, Neoguillauminiinae, and Euphorbiinae. Within Euphorbiinae, there are four major clades, only one of which corresponds with a previously recognized taxon; the three remaining clades are conglomerates of various subgenera and sections. The majority of the subtribe is composed of a paraphyletic *Euphorbia*. All other genera currently recognized in the subtribe are nested within *Euphorbia*. In addition, *Synadenium* and *Endadenium* are nested within *Monadenium*. Within *Euphorbia*, the majority of the currently recognized subgenera are either paraphyletic or polyphyletic. Biogeographical patterns examined in light of the molecular evidence suggest that the tribe Euphorbieae arose in Africa, possibly before the breakup of Gondwanaland, at which time the major lineages of subtribe

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Euphorbiinae were already present. It is argued that the best solution for *Euphorbia* classification is a broad circumscription of *Euphorbia* that contains all of the about 2000 species of the subtribe Euphorbiinae.

Key words: classification, *Euphorbia*, Euphorbieae, ITS, *ndh*F.

It was only a year after Linnaeus (1753) first circumscribed the genus *Euphorbia* L. (Euphorbiaceae) to include all of the then-known members of the tribe Euphorbieae that other botanists began to divide the genus into several smaller genera (Miller, 1754; Trew, 1754). The controversy has continued since, and almost 250 years later the issue as to whether *Euphorbia* should be recognized in its initial broad sense or be separated into many smaller genera still has not been resolved. *Euphorbia* and Euphorbieae are generally considered taxonomically difficult, and a considerable degree of uncertainty has always existed about the relationships of the groups within them. This problem is due in great part to extreme morphological diversity, a large number of species, and a subcosmopolitan distribution. Few workers have been able to gain a complete understanding of the tribe throughout its immense range, and there has never been a universally accepted classification. This lack of consistency has hindered and to some extent discouraged research within the genus *Euphorbia* as well as the Euphorbieae as a whole. Thus, a clear understanding of relationships within the tribe is of great importance in order to provide subsequent workers with a phylogenetic framework on which to base their studies.

The tribe Euphorbieae is characterized by its synapomorphic pseudanthial inflorescence (termed a cyathium) composed of a gland-bearing involucre of several united bracts and their associated flowers and bracteoles. Each bract subtends a monochasial staminate inflorescence, and these monochasia surround a single pistillate flower. The individual flowers in Euphorbieae are highly reduced and represented by a single stamen or ovary, with or without a perianth. The staminate flowers terminate slender pedicels, and the pistillate flowers can be long-pedicellate or subsessile. This structure is highly complex, and there are still doubts as to its exact nature and evolution (Gilbert, 1994).

According to the most recent synopsis of the Euphorbiaceae (Webster, 1994), the Euphorbieae contain 11 genera placed into three subtribes: Anthosteminae (Baill.) G. L. Webster, Neoguillauminiinae Croizat, and Euphorbiinae. The presence or absence of a perianth (presumably a calyx) on the flowers distinguishes these taxa. In Anthosteminae both the staminate and pistillate flowers possess a perianth; in Neoguillauminiinae only the pistillate flowers possess a perianth; and in Euphorbiinae neither the pistillate nor the staminate flowers possess a well-developed perianth, although a rudimentary calyx-like structure is present below the pistillate flowers in a few species.

Anthosteminae consist of two genera of tropical forest trees: *Anthostema* A. Juss. (4 spp. disjunct in west tropical Africa and Madagascar) and *Dichostemma* Pierre (1 sp. in west tropical Africa). This subtribe is considered the least specialized because of the perianth on both the staminate and pistillate flowers. Further, each individual involucral bract closely envelops a cluster of many bracteoles and staminate flowers. The cyathia are bisexual or staminate. In *Anthostema* the cyathia are arranged in condensed axillary cymes. The involucre is made up of four united bracts and is slightly zygomorphic because it is spread in an open half circle. There are five large glands along the involucral bract margins and between the clusters of staminate flowers. The 3-locular pistillate flower is not contained in the involucre but instead lies at the base of the involucre's open side. Based on its open involucral morphology and the possible lateral position of the pistillate flower, this genus probably most closely resembles the ancestral inflorescence morphology of the Euphorbieae. In *Dichostemma* the cyathia are arranged in loose, open, axillary or terminal cymes. In contrast to *Anthostema*, the four monochasia-containing involucral bracts are united in a ring, and the involucre is completely closed and actinomorphic. The four involucral glands are contained within this structure and attached to the inner walls of the bracts and the base of the gynophore. In the center of the inflorescence is either a minute pistillode or a 4-locular pistillate flower.

Like Anthosteminae, the subtribe Neoguillauminiinae also contains two genera: *Calycopeplus* (5 spp. in Australia) and *Neoguillauminia* Croizat (1 sp. in New Caledonia). In contrast to Anthosteminae, the staminate flowers lack a perianth. However, a perianth is present on the pistillate flower, and this combination of features defines the subtribe. In addition, the bracts of the involucre do not tightly envelop the staminate monochasia, although the latter are enclosed within large bracteoles. *Calycopeplus* are xerophytic shrubs with small, oppo-

site leaves and cyathia arranged in axillary clusters. The involucre is distinctly cupular and is made up of four bracts. The glands are located between the lobes and attached to the wall of the cupular involucre. There is a central pistillate flower surrounded by four staminate monochasia that are opposite the involucral lobes. The sole representative of *Neoguillauminia* is a mesic forest tree or shrub with large, spirally arranged leaves. The cyathia are long-pedunculate and arranged in few-cyathiate axillary or subterminal groups. The involucre is composed of four to six bracts that extend into large, petaloid appendages. There are eight to twelve glands arranged in pairs between the four to six staminate monochasia and attached to the base of the involucre and sometimes also to the base of the gynophore. There is a single central pistillate flower. *Neoguillauminia* is noteworthy because the involucres are generally composed of five bracts, and a 5-merous involucre also characterizes Euphorbiinae, discussed below. *Calycopeplus*, as well as *Anthostema* and *Dichostemma*, possess 4-merous involucres.

With about 2000 species and a subcosmopolitan distribution, the largest and most complex subtribe is Euphorbiinae. It is characterized by the lack of a perianth on both the staminate and pistillate flowers, although a rudimentary calyx-like structure is present below the pistillate flowers of a few species. In addition, the involucre is made up of five united bracts, not four as generally are found in the other subtribes of Euphorbieae, and the bracteoles that surround the staminate monochasia are generally reduced. The glands are mostly located along the rim of a cupular involucre. Again following the circumscription of Webster (1994), the subtribe contains seven genera: *Chamaesyce* Gray, *Cubanthus* (Boiss.) Millsp., *Endadenium* Leach, *Euphorbia*, *Monadenium* Pax, *Pedilanthus* Necker ex Poit., and *Synadenium* Boiss. *Poinsettia* Graham and *Elaeophorbia* Stapf are also sometimes recognized as distinct from *Euphorbia*, but their status is not as widely accepted, and most authors treat these as infrageneric taxa of *Euphorbia*. Extreme emphasis is placed on variation in the configuration of the cyathium, and with the exception of *Chamaesyce*, the genera segregated from *Euphorbia* are distinguished on the basis of involucral features.

Euphorbiinae are dominated by *Euphorbia*, which accounts for ca. 80% of the species and occurs throughout the geographic range of the subtribe. The genus is best known for the common Christmas poinsettia (*Euphorbia pulcherrima* Willd. ex Klotzsch) and is popular with horticulturists because of the prevalence of succulents. One of the most fascinating features of the subtribe is its great diversity of growth forms. Large forest trees, shrubs, perennial herbs, geophytes, annuals, and a great diversity of succulents are all well represented. In comparison to most other genera of Euphorbiinae, the cyathial morphology of *Euphorbia* is relatively unspecialized. The cyathia are actinomorphic and generally possess one to five separate glands situated on the rim of the involucre, and this plesiomorphic feature unites the genus.

With about 300 species, *Chamaesyce* is the largest segregate genus from *Euphorbia*. It occurs widely, but most species are confined to the New World. Distinguished on the basis of vegetative morphology, its cyathia are nearly identical to those of many species of *Euphorbia* subg. *Agaloma* (Raf.) House. *Chamaesyce* is characterized by many unusual synapomorphies: apical abortion of the main shoot and subsequent sympodial growth; interpetiolar stipules; opposite, frequently asymmetrical leaves; and C_4 photosynthesis (Koutnik, 1984, 1987). Numerous Euphorbieae specialists (e.g., Carter, 1988a, 1992b; Gilbert, 1987) retain it as a subgenus of *Euphorbia*.

The other five segregate genera of *Euphorbia* are also easily identifiable, but their differences, as mentioned above, involve involucral features. Three genera possess zygomorphic cyathia: in *Pedilanthus* (15 spp., primarily Mexico) there are two to six glands enclosed within an adaxial, spurlike extension of the involucre; in *Cubanthus* (3 spp., Cuba and Hispaniola) there are two glands united into a shieldlike structure on the outside of the involucre; and in *Monadenium* (ca. 70 spp., Africa) the glands are united into a single horseshoe-shaped structure. The two remaining segregate genera possess actinomorphic cyathia: in *Synadenium* (20 spp., Africa) the cyathia possess five united glands that form a complete ring around the top, and in *Endadenium* (1 sp., Angola) the closed rim of the cyathium is not a gland but instead an apparently eglandular extension of the involucral wall with a ring of nectar-bearing depressions on the inside of the involucre.

Taxonomic History of the Tribe Euphorbieae

The taxonomic works treating Euphorbieae are numerous, and only a brief overview, focusing on those with broad and significant implications to modern Euphorbieae taxonomy, will be provided here. A more detailed account is found in Steinmann (2001).

One of the first prominent taxonomic treatments of the Euphorbieae was that of Klotzsch and Garcke

(1859, 1860). Although these authors segregated both *Anthostema* and *Pedilanthus* into separate tribes, the Anthostemeae and Pedilantheae, they did concede their close relationship with Euphorbieae. Their Euphorbieae contained 408 species, all members of present-day Euphorbiinae. *Euphorbia* was recognized in a restricted sense, with only 27 species. The remainder were placed in 17 segregate genera, organized in two subtribes: Anisophyllae Klotzsch & Garcke and Tithymalae Klotzsch & Garcke.

The first and last monograph of the entire Euphorbieae, and the basic framework for the classification that is still in use today, was provided by Boissier in 1862 (supplement 1866) for de Candolle's *Prodromus*. Boissier followed Klotzsch and Garcke by recognizing Anthostemeae as distinct, but differed from them by submerging Pedilantheae into Euphorbieae. Euphorbieae contained 740 species. Also in contrast to Klotzsch and Garcke, Boissier recognized *Euphorbia* in a broad sense, and his Euphorbieae contained only three genera, all currently placed in Euphorbiinae: *Pedilanthus* (15 spp.), *Synadenium* (2 spp.), and *Euphorbia* (723 spp.). The taxa of *Euphorbia* were positioned into 27 sections and two "series": Appendiculatae Boiss. (corresponding to Klotzsch and Garcke's subtribe Anisophyllae) and Exappendiculatae Boiss. (corresponding to Klotzsch and Garcke's subtribe Tithymalae). *Calycopeplus* and *Neoguillauminia* were treated in *Euphorbia*, and *Cubanthus* was erected as a section of *Pedilanthus*.

Bentham (1878) expounded greatly on the Euphorbiaceae as a prelude to his treatment of the family in *Genera Plantarum* (Bentham, 1880). He agreed that *Euphorbia* should be recognized in the broad sense and followed Boissier's treatment with only minor modifications. Anthostemae was combined with Euphorbieae. *Calycopeplus*, first described by Planchon in 1861 but subsequently treated as a synonym of *Euphorbia* by Boissier (1862), was resurrected at the rank of genus. Bentham's greatest change concerned the rank of Boissier's sections of *Euphorbia*, and he proposed a system containing only six sections, under which the majority of Boissier's sections were reduced to subsections. Otherwise, Bentham did little to modify Boissier's grouping of species.

Around the turn of the century, Pax (1894a) described *Monadenium* and Pierre (1896) described *Dichostemma*, the second known genus in the modern subtribe Anthosteminae. Nearly two decades later, Millspaugh (1913) first recognized *Cubanthus* as a distinct genus.

The next major treatment of the Euphorbieae was that of Pax and Hoffmann (1931) in Engler's *Die natürlichen Pflanzenfamilien*. They essentially followed Bentham's classification with only minor modifications to accommodate newly described taxa. Again, a single tribe, the Euphorbieae, was recognized without any further divisions. *Anthostema*, *Dichostemma*, and *Calycopeplus* were all treated as distinct. *Euphorbia* continued to be recognized in the broad sense, although the number of segregate genera had increased. In addition to the earlier recognized *Pedilanthus* and *Synadenium*, these authors segregated the genera *Monadenium*, *Stenadenium* Pax, *Elaeophorbia*, and *Diplocyathium* H. Schmidt. The latter two segregates are now treated within *Euphorbia* (Webster, 1994), and *Stenadenium* is currently treated as a synonym of *Monadenium* (Bally, 1959, 1961). *Cubanthus* was relegated back to a section of *Pedilanthus*.

In 1937, Croizat described the genus *Neoguillauminia* and the subtribe Neoguillauminiinae to accommodate it. The type, *N. cleopatra*, was first described by Baillon (1861) as a species of *Euphorbia* and placed in his monotypic *E.* sect. *Decadenia* Baill. Boissier (1862) treated this species within *E.* sect. *Tithymalus*.

Shortly after Croizat's contribution, Wheeler (1943) published a broad classification of the entire Euphorbieae. This was the first major conspectus to advocate the use of subgenus as the primary division of *Euphorbia*, and it is this rank that predominates in current Euphorbiinae classification. Wheeler recognized a single Euphorbieae but abandoned Croizat's subtribes. The genera that he included were the same as those of Pax and Hoffmann (1931) except that *Diplocyathium* was relegated to synonymy within *Euphorbia*, and Croizat's newly described *Neoguillauminia* was recognized. *Euphorbia* consisted of eight subgenera, and in general, these corresponded to the sections recognized by Pax and Hoffmann (1931).

Dressler (1957) provided a monograph of *Pedilanthus* in which he convincingly demonstrated that the species of *Cubanthus* do not belong within *Pedilanthus* and should be treated separately. Dressler is also noteworthy because he advocated that *Euphorbia* should be recognized in the narrow sense and restricted to Old World succulents.

In the years after Dressler's treatment, Webster made important contributions to Euphorbieae taxonomy. He suggested the recognition of *Chamaesyce* as a genus and at the same time strongly suggested that *Elaeophorbia* should be treated within *Euphorbia* (Webster, 1967). Eight years later, Webster (1975) circumscribed the tribe to its present, generally accepted configuration. He created the

subtribe Anthosteminae to accommodate *Anthostema* and *Dichostemma* and resurrected Neoguillauminiinae to include *Calycopeplus* and *Neoguillauminia*. In his third subtribe Euphorbiinae, he recognized seven genera: *Euphorbia, Chamaesyce, Cubanthus, Endadenium, Monadenium, Pedilanthus,* and *Synadenium.*

Gilbert (1987) and Carter (1985, 1988a) have made the most recent modifications in Euphorbiinae classification. Their changes primarily involve African members and the elevation of various previously recognized sections of *Euphorbia* to subgeneric rank.

In summary, at the time of this writing most authors agree that Euphorbieae is a single tribe with three subtribes: the Anthosteminae, the Neoguillauminiinae, and the Euphorbiinae. Within Anthosteminae there are two genera, *Anthostema* and *Dichostemma.* Within Neoguillauminiinae there are also two genera, *Calycopeplus* and *Neoguillauminia.* The subtribe Euphorbiinae contains about seven genera. Those that are universally accepted are *Euphorbia, Endadenium, Monadenium, Synadenium, Pedilanthus,* and *Cubanthus.* Genera that are less frequently accepted are *Chamaescye, Elaeophorbia,* and *Poinsettia.* Other segregate genera have not even gained minor acceptance. Within *Euphorbia,* the common primary division employed is the rank of subgenus, and there are 9 to 11 generally recognized subgenera: *Agaloma, Chamaesyce* Raf. (when not treated as a genus), *Poinsettia* (Graham) House (when not treated as a genus), *Esula* Pers., *Eremophyton* (Boiss.) L. C. Wheeler, *Euphorbia, Lacanthis* (Raf.) M. G. Gilbert, *Tirucalli* (Boiss.) S. Carter, *Trichadenia* (Pax) S. Carter, *Rhizanthium* (Boiss.) L. C. Wheeler, and *Lyciopsis* (Boiss.) L. C. Wheeler. However, a modern, global, coherent classification of the genus is lacking, and some proposed sections of *Euphorbia* have not been adequately accommodated within a currently recognized subgenus (e.g., *E.* sects. *Arthrothamnus* (Klotzsch & Garcke) Boiss., *Denisophorbia* (Leandri) Croizat, and *Deuterocalli* Croizat). Detailed accounts of the currently recognized infrageneric taxa of *Euphorbia* and their taxonomic histories are presented in the discussion section.

Materials and Methods

In total, 227 species were sampled (Appendix 1), including 4 outgroup and 223 ingroup species. Outgroups were chosen from tribe Hippomaneae because it is traditionally considered to be closely related to the Euphorbieae (Webster, 1994), and a broad molecular phylogenetic reconstruction of the entire Euphorbiaceae also supports their affinity (Kenneth Wurdack, pers. comm.). An attempt was made to include as broad a sample as possible from Euphorbieae. Four species of Anthosteminae, 4 species of Neoguillauminiinae, and 215 species of Euphorbiinae were sequenced. These included all genera (except *Cubanthus*) recognized by Webster (1994). The sole representative of *Endadenium,* eight species of *Pedilanthus,* one species of *Synadenium,* eight species of *Chamaesyce,* and five species of *Monadenium* were included. One hundred ninety-two species of *Euphorbia* were represented, including all sections (except sects. *Bongium* Boiss. and *Caulanthium* Boiss.) treated by Boissier (1862) and most other important taxonomic groups recognized by subsequent workers (e.g., Webster, 1967; Gilbert, 1987; Carter, 1985, 1988a).

The ITS analysis included 216 species (4 outgroups, 3 Anthosteminae, 2 Neoguillauminiinae, and 207 Euphorbiinae). The sample for the *ndh*F analysis was smaller and included 114 species (4 outgroups, 4 Anthosteminae, 3 Neoguillauminiinae, and 103 Euphorbiinae). Following a preliminary analysis of the ITS sequence data, a subset of the sampled taxa representing the major clades and well-supported lineages was sequenced for the *ndh*F analysis. In addition, 15 species were included in the *ndh*F analysis that were not included in the ITS analysis because of problems obtaining "clean" ITS sequences for these taxa (see Appendix 1).

Total genomic DNA was isolated from either fresh, silica gel-dried, or herbarium material using a modified CTAB method (Doyle & Doyle, 1987). Two genic regions were employed in the phylogenetic reconstructions: the cpDNA coding region *ndh*F and the nrDNA internal transcribed spacer region (ITS). ITS amplification using the polymerase chain reaction (PCR) followed the procedures described by Baldwin (1992) and Baldwin et al. (1995). Amplification of the *ndh*F region generally followed the protocols described by Olmstead and Sweere (1994) and Kim and Jansen (1995). The 5′ quarter of the *ndh*F region was excluded due to problems amplifying it. Also, a primer ca. 50 bp internal to the 3′ end "2110Ri" (5′-TCA ATT ATT CGT TTA TCA A-3′) was designed because many taxa would not amplify using primer "2110R." Four additional primers were specifically designed for this study: (1) (5′-TTA TTC AAT ATC TYT ATG GGG TAA-3′), (2) (5′-TAA CCC CAT ARA GAT ATT GAA TAA-3′), (3) (5′-TAG GAA TTC CYT TYA ATC AA-3′), and (4) (5′-TTG ATT RAA RGG AAT TCC TA-3′).

The PCR products were electrophoresed using a

Table 1. Characteristics of the ITS and portion of the *ndh*F regions included in this study.

	ITS	ITS1	5.8s	ITS2	*ndh*F
Raw length (bp)	591–660	210–267	164–167	202–241	1467–1506
Aligned length	739	303	169	267	1587
Variable sites (proportion)	527 (0.71)	272 (0.90)	35 (0.21)	220 (0.82)	740 (0.47)
Parsimony-informative sites (proportion)	470 (0.64)	244 (0.81)	22 (0.13)	204 (0.76)	519 (0.33)
GC content, mean (range)	0.58 (0.50–0.70)	0.58 (0.46–0.71)	0.56 (0.51–0.58)	0.61 (0.48–0.76)	0.32 (0.30–0.33)

1.5% agrose gel in a 0.5x TBE (pH 8.3) buffer, stained with ethidium bromide, and then cleaned using the PEG precipitation protocol (Nickrent, 1996). Cycle-sequencing adhered to the manufacturer's specification using the PRISM™ Dye-Deoxy™ Terminator Kit (Perkin-Elmer, Inc.). Cycle-sequencing was followed by ethanol purification, and sequencing used an Applied Biosystems Model 373A Automated DNA Sequencing System.

Sequences were assembled from automated DNA sequence chromatograms using Sequencher 3.0 (Gene Codes Corporation, Inc.). ITS sequences were initially aligned with ClustalW v. 1.4 (Thompson et al., 1994), using a gap cost:gap extension cost ratio of 10:5, followed by visual modifications; *ndh*F sequences were aligned visually. Because of high divergence and the large number of taxa included in the study, alignment was problematic for certain highly variable regions of ITS sequences. However, the difficulties mostly occurred aligning the major lineages of Euphorbieae to each other, and alignment within major lineages was less problematic. Alignment of both ITS and *ndh*F introduced gaps into some sequences, and these sites were included in the analyses. Missing data were coded with a question mark in the matrix. Alignment matrices have been deposited at the library of Rancho Santa Ana Botanic Garden and submitted to TreeBASE (http://herbaria.harvard.edu/treebase.index.html).

The aligned ITS and *ndh*F sequence matrices were analyzed separately using PAUP* 4.0b4a for Macintosh™ (Swofford, 2000) on a Macintosh™ G3. Due to the large data sets, maximum parsimony using heuristic searches (Acctran, 10 random addition cycles, TBR branch swapping, steepest descent option not in effect) was employed. Maximum likelihood estimates of transition/transversion (TI/TV) biases were measured for both the ITS and *ndh*F data sets individually as implemented in PAUP* 4.0b4a under the HKY model of nucleotide substitution and using the equal-weighted parsimony trees. These estimates were used to produce a TI/TV step matrix, employed in further maximum parsimony analyses. This weighting scheme was employed in order to model more closely the maximum parsimony analyses to the given data set. Indels were coded as missing data. Multiple most parsimonious trees were combined in a strict consensus tree. Tree robustness was estimated using 10,000 "fast addition" heuristic bootstrap replicates.

Results

Sequence variation for both ITS and *ndh*F is shown in Table 1. For ITS sequences, pairwise levels of divergence (uncorrected "p" values) for the entire Euphorbieae ranged from 34.4% (between *Anthostema* sp. nov. and *Euphorbia insulana*) to 1.1% (between *E. alta* and *E. spathulata*). For subtribe Anthosteminae, levels of divergence varied from 9.4% (between *Dichostemma glaucescens* and *Anthostema madagascariense*) to 2.2% (between *A. madagascariense* and *A.* sp. nov.); for the two included species of subtribe Neoguillauminiinae (*Neoguillauminia cleopatra* and *Calycopeplus casuarinoides*), the level of divergence was 7.6%; for subtribe Euphorbiinae levels of divergence varied from 30.9% (between *E. trichotoma* and *E. panchganiensis*) to 1.1% (between *E. alta* and *E. spathulata*). As expected, levels of divergence for *ndh*F sequences were much lower than levels observed in ITS sequences. For the entire Euphorbieae, these ranged from 11.7% (between *Anthostema* sp. nov. and *E. oaxacana*) to 0.1% (between *E. bilobata* and *E. exstipulata*). For subtribe Anthosteminae, levels of divergence varied from 2.6% (between *Anthostema* sp. nov. and *Dichostemma glaucescens*) to 0.4% (between *Anthostema* sp. nov. and *A. madagascariense*); for subtribe Neoguillauminiinae divergence levels varied from 2% (between *Calycopeplus collinus* and *C. paucifolius*) to 1.4% (between *Neoguillauminia cleopatra* and *Calycopeplus paucifolius*); for subtribe Euphorbiinae levels of divergence varied from 9.6% (between *E. aphylla* and

Table 2. Statistics from weighted maximum parsimony analyses of ITS and *ndh*F datasets and statistics for unweighted characters of the same topology. For each analysis, number and length of most parsimonious trees, consistency index (CI), retention index (RI), and rescaled consistency index (RC) are reported.

Analysis	Number of trees	Tree length	CI	RI	RC
ITS (weighted)	2160	8838.2	0.1813	0.7219	0.1309
ITS (unweighted)	2160	6887	0.1802	0.7126	0.1284
*ndh*F (weighted)	19012	1818.2	0.5221	0.7926	0.4138
*ndh*F (unweighted)	19012	1985	0.5441	0.7992	0.4349

E. oaxacana) to 0.1% (between *E. bilobata* and *E. exstipulata*).

Transition/transversion biases were calculated to be 1.8 for the ITS data set and 0.85 for the *ndh*F data set. These biases were used in the weighted maximum parsimony analyses.

The ITS analysis resulted in the recovery of 2160 most parsimonious trees of 6887 steps (equal weighted). The *ndh*F analysis resulted in the recovery of 19,012 most parsimonious trees of 1985 steps (equal weighted). Statistics for both analyses are detailed in Table 2. The strict consensus of the 2160 trees obtained in the ITS analysis is depicted in Figures 1, 5, 7, 9, 10, 12, and 13. The strict consensus of the 19012 trees obtained in the *ndh*F analysis is depicted in Figures 2, 6, 8, 11, and 14. With the exception of Figures 3 and 4, phylograms are presented in Steinmann (2001).

For the ITS analysis, the bootstrap 50% majority rule tree (values depicted on strict consensus tree) is structurally identical to the strict consensus insofar as the majority rule tree is resolved. Many of the terminal clades are supported with high bootstrap (bs) percentage values. However, there is no support for the majority of the basal internal nodes. Notable exceptions are the ancestral nodes that define the tribe Euphorbieae and its subtribes. In the *ndh*F analysis, the bootstrap 50% majority rule tree (values depicted on strict consensus tree in Fig. 2) is structurally identical to the strict consensus with one significant difference. In the bootstrap analysis, clade A is not placed as the sister taxon of clade B but instead is located at the earliest diverging clade in a group that contains clades C and D, and this is supported by a bootstrap value of 77%. This incongruency suggests that the topology of the major clades within the subtribe Euphorbiinae should be viewed with caution. The majority of clades found in the *ndh*F strict consensus tree are supported in the bootstrap analysis, and in contrast to ITS (see Fig. 1), many of the internal, basal nodes also possess significant bootstrap support.

It is worth noting that a combined analysis was conducted for the 99 species in common between the ITS and *ndh*F data sets. The results are not presented here because results from the independent ITS and *ndh*F analyses agree strongly with each other, and the combined analysis does not provide novel insights. For the instances in which tree structure resulting from the ITS and *ndh*F analyses differed, the combined analysis generally provided the same structure as the *ndh*F analysis.

Discussion

Utility of the *ndh*F and ITS regions in Euphorbiaceae and a comparison of the resulting phylogenies

Despite being one of the largest angiosperm families and an important floristic component, especially in tropical regions, the Euphorbiaceae have not previously been the subject of a comprehensive molecular systematics investigation. If the results obtained here are any indication, both *ndh*F and the ITS data appear useful in inferring relationships within the family. In general, the two reconstructions of the Euphorbieae are similar, and thus corroborate evidence of their phylogenetic signal. The overall structure of both analyses is the same (Figs. 1, 2), and when differences do occur, these generally involve clades that lack bootstrap support in one or both of the analyses. There are very few instances in which well-supported clades are positioned differently in the separate analyses, e.g., the arrangement of *Euphorbia meenae* Blatt. & McCann, *E. abdelkuri* Balf.f., *E. drupifera* Thonn., and *E. poissonii* Pax (Figs. 10, 11).

Monophyly of the Euphorbieae and its subtribes and paraphyly within subtribe Euphorbiinae

In both analyses, Euphorbieae form a monophyletic assemblage with respect to the four outgroups. However, there is not high bootstrap support for this grouping in either analysis. The unusual synapo-

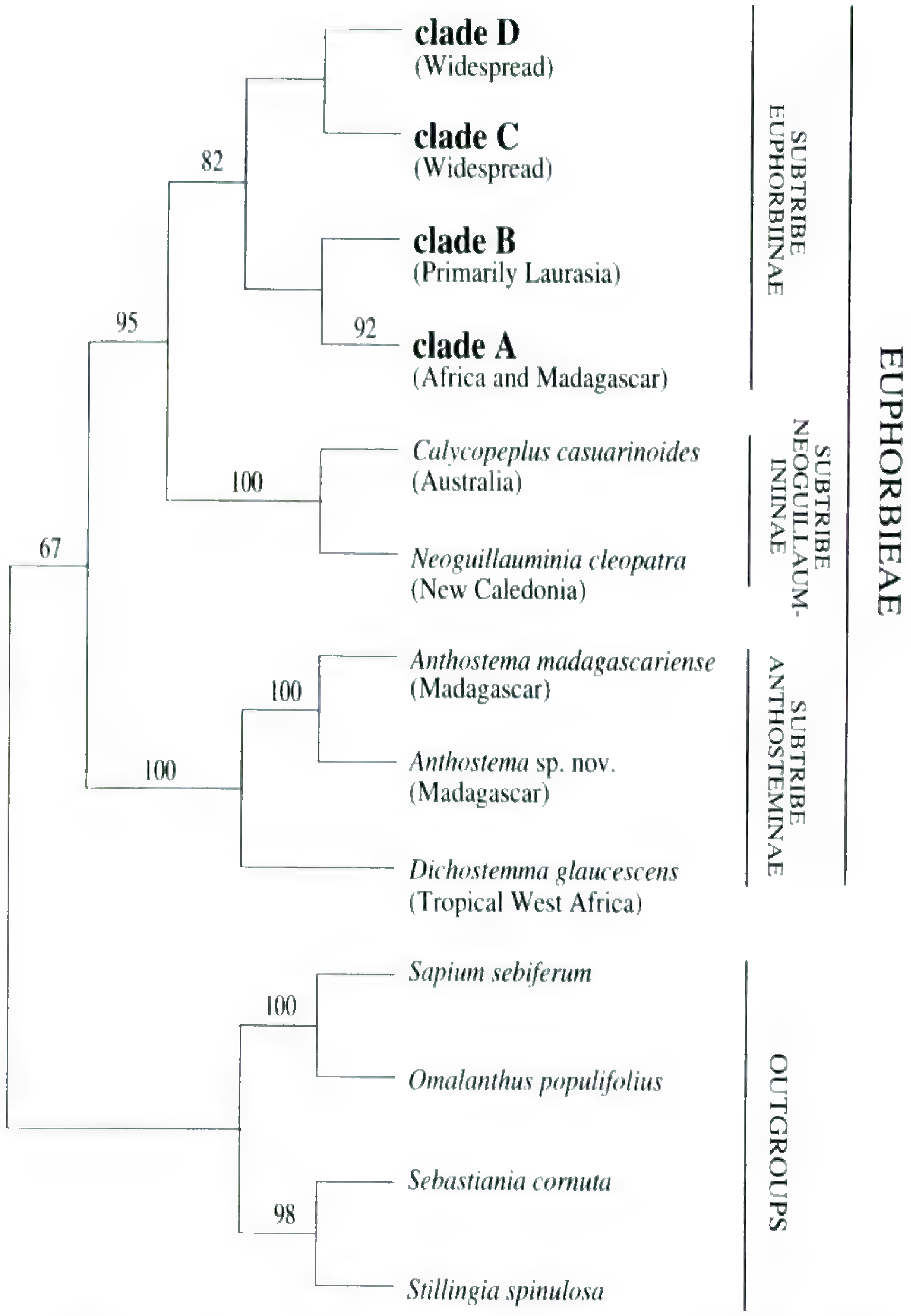

Figure 1. Strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. The tribes and subtribes of the classification of Webster (1994) are indicated. Individual strict consensuses for clades A–D are found in Figures 5, 7, 9, 10, 12, and 13.

morphic inflorescence structure of the tribe therefore supports this relationship, and it is highly probable that the tribe is indeed monophyletic. All three subtribes of Euphorbieae also form monophyletic groups (Figs. 1, 2), and these clades possess high bootstrap support, 100% for all three in the *ndh*F analysis. Further, in both analyses subtribe Anthosteminae is the earliest diverging subtribe in Euphorbieae and subtribes Neoguillauminiinae and Euphorbiinae are sister to each other. *Anthostema* and *Calycopeplus* are strongly supported to be monophyletic (bs 100% and 90% in *ndh*F, respectively), and presumably so too are the monotypic *Dichostemma* and *Neoguillauminia*. Therefore, Webster's overall classification of the tribe Euphorbieae (1975) is consistent with the molecular results.

Within Euphorbiinae, both analyses demonstrate that *Chamaesyce, Pedilanthus, Monadenium, Synadenium*, and *Endadenium* are all nested within a paraphyletic *Euphorbia* (see clades C and D, Figs. 9–14). Also, both *Synadenium* and *Endadenium* are nested within a paraphyletic *Monadenium*.

RELATIONSHIPS AND MAJOR LINEAGES WITHIN THE EUPHORBIINAE

Both analyses support that there are four major lineages within the subtribe Euphorbiinae, here

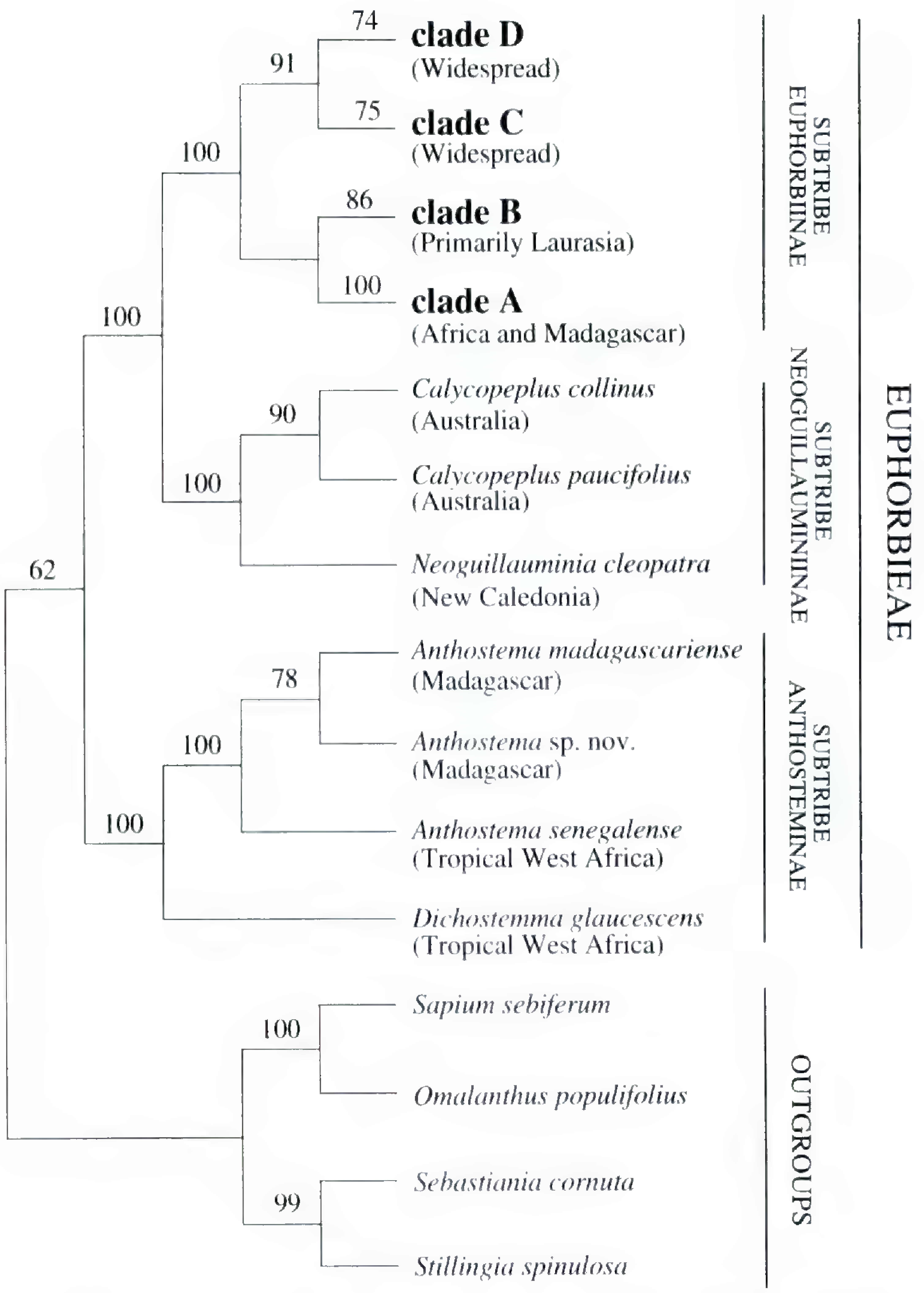

Figure 2. Strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. The tribes and subtribes of the classification of Webster (1994) are indicated. Individual strict consensuses for clades A–D are found in Figures 6, 8, 11, and 14.

designated clades A–D. With the exception of clade B (primarily composed of the temperate herbaceous group of *Euphorbia* subg. *Esula*), none of these lineages closely correspond to any previously recognized taxon. Instead, they are conglomerates of various sections and subgenera. All of these major lineages possess significant bootstrap support in the *ndh*F analysis (bs 74–100%), while only clade A is supported in the ITS analysis (bs 92%). There still is some question, however, as to the exact relationship among these lineages. Although both the ITS and *ndh*F strict consensus trees show that clades A and B are sister to each other and together these are sister to clades C and D, there is no bootstrap support to this grouping in either analysis.

Due to the lack of a comprehensive classification, many sections of *Euphorbia* have not been accommodated within a currently recognized subgenus. Also, some sections that have been suggested to belong to a particular subgenus are demonstrated to not be closely related. Therefore, the following discussion about the major groups of Euphorbiinae is organized by taxa of various ranks.

Chamaesyce. Eight species from *Chamaesyce* were included. In both the ITS and *ndh*F analyses (Figs. 12, 14), these species form a well-supported, monophyletic group (bs 91% and 99%, respectively) in clade D. Species previously thought to intergrade with *Chamaesyce* (see Webster, 1967), such

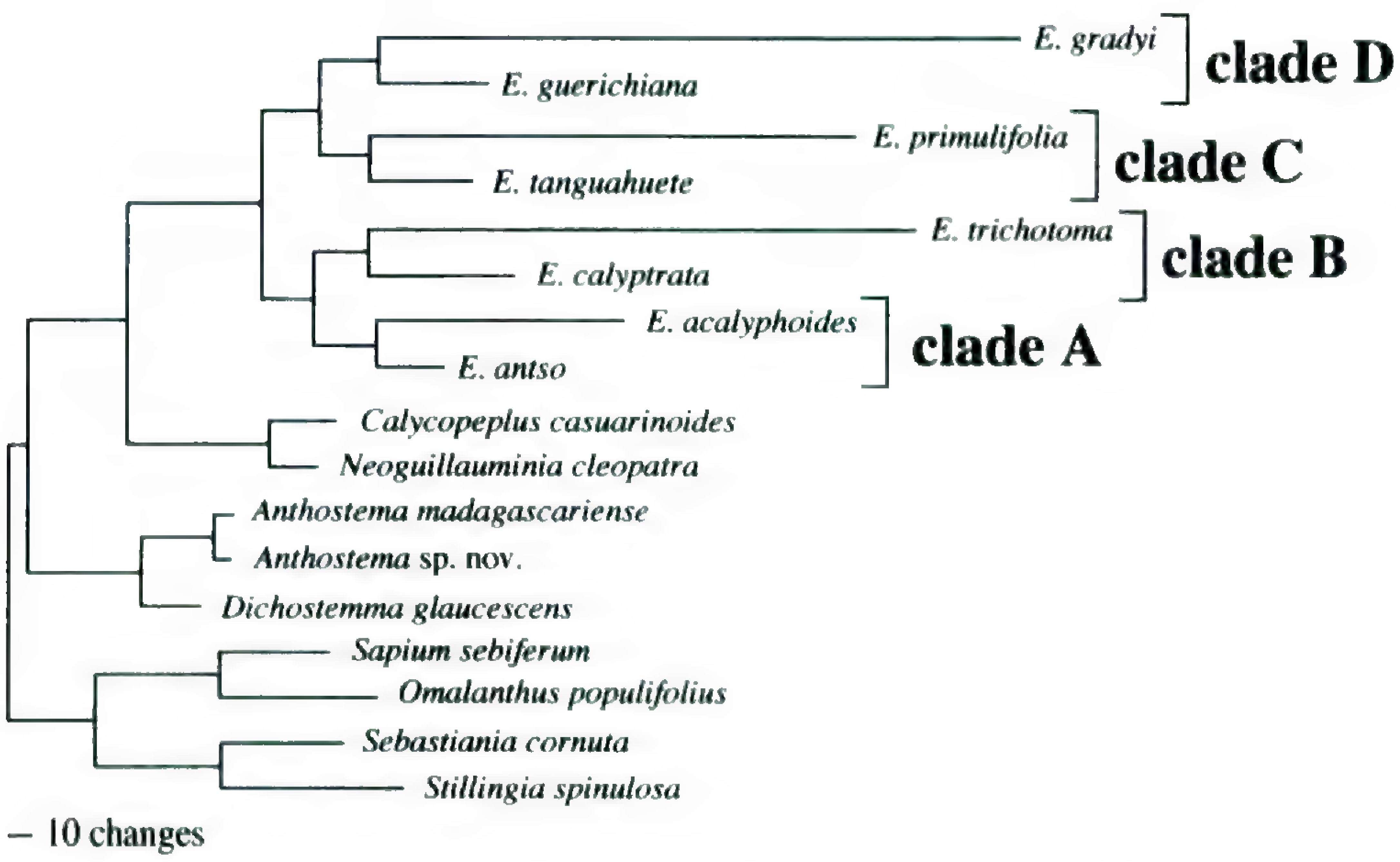

Figure 3. Phylogram of one of the equally most parsimonious trees resulting from the ITS analysis, showing branch lengths within Euphorbieae. Only the species with the least and most changes are shown for each of the major clades of subtribe Euphorbiinae. Individual phylograms of clades A–D are given in Steinmann (2001). *E.* = *Euphorbia.*

as *Euphorbia innocua* L. C. Wheeler and *E. peperomioides* Boiss., appear to share their vegetative similarity due to convergence, as they do not group close to the *Chamaesyce* clade (Figs. 9, 12, 13). Similarly, *E. cheirolepis* Fisch. & C. A. Mey., suggested by Prokhanof (1949) to be possibly intermediate between *Chamaesyce* and other species of *Euphorbia,* is not supported to be closely related (Figs. 12, 14). At least based on the molecular results, these putative relatives are clearly outside *Chamaesyce,* and the characters presented in the introduction can distinguish all true species of *Chamaesyce.* As previously suggested by Dressler (1957) and Webster (1967), *Chamaesyce* is derived from within *E.* subg. *Agaloma* (Figs. 12, 14).

Sampling of *Chamaesyce* was not broad enough to determine the monophyly of the subsections proposed by Boissier (1862). However, it is noteworthy that *C. acuta* and *C. angusta,* both in *Chamaesyce* subsect. *Acutae* Boiss., lie sister to the remainder of the species sampled from *Chamaesyce* subsects. *Gymnadeniae* Boiss., *Cheloneae* Boiss., *Chamaesyce,* and *Hypericifoliae* Boiss. *Chamaesyce* subsect. *Acutae* is the only group within *Chamaesyce* not possessing the derived C_4 photosynthetic pathway otherwise characteristic of the genus (Webster et al., 1975; Mayfield, 1991).

Synadenium/Monadenium/Endadenium. Although their composition differs between the ITS and *ndh*F analyses, a total of six species from these genera, here referred to as the *Synadenium* alliance, were included. They form a well-supported, monophyletic group (bs 100% in both analyses, see Figs. 10, 11). Both ITS and *ndh*F also suggest that *Monadenium* is paraphyletic with *Synadenium* and *Endadenium* nested inside it. Morphologically, the genera are united in the possession of fused involucral glands. They belong to a well-supported clade C (bs 78% in ITS, 100% in *ndh*F) that also contains *Euphorbia* subg. *Euphorbia* and *Lacanthis.*

Pedilanthus. As their unusual zygomorphic cyathia suggest, the eight species of *Pedilanthus* included here form a well-supported (bs 100% in both analyses), monophyletic group (Figs. 9, 11). Based primarily on its involucral appendages and predominantly Mexican distribution, Dressler (1957) and Webster (1967) suggested that *Pedilanthus* arose from *Euphorbia* subg. *Agaloma,* with *E. fulgens* Karw. ex Klotzsch as the closest potential living intermediate. However, this analysis does not support any relationship between these two groups. In fact, they do not even belong to the same major clade of Euphorbiinae, with *E. fulgens* (Fig. 13) and other members of subgenus *Agaloma* (Figs. 11–13) belonging to clade D. Beyond being a member of clade C, the exact position of *Pedilanthus* is not strongly supported. In the ITS analysis (Figs. 9, 10), it lies sister to the clade of Old World taxa that includes the *Synadenium* alliance and *E.* subg. *Euphorbia* and *Lacanthis.* However, there is no bootstrap support for the relationship. The *ndh*F analysis (Fig. 11) suggests a relationship with *E. elata* in a weakly supported clade (bs 72%) of various Neotropical species. At least based on biogeography, this association is more plausible. Involucral appendages have arisen on various occasions within Euphorbiinae, and their presence in *Pedilanthus* apparently represents an independent derivation of this feature.

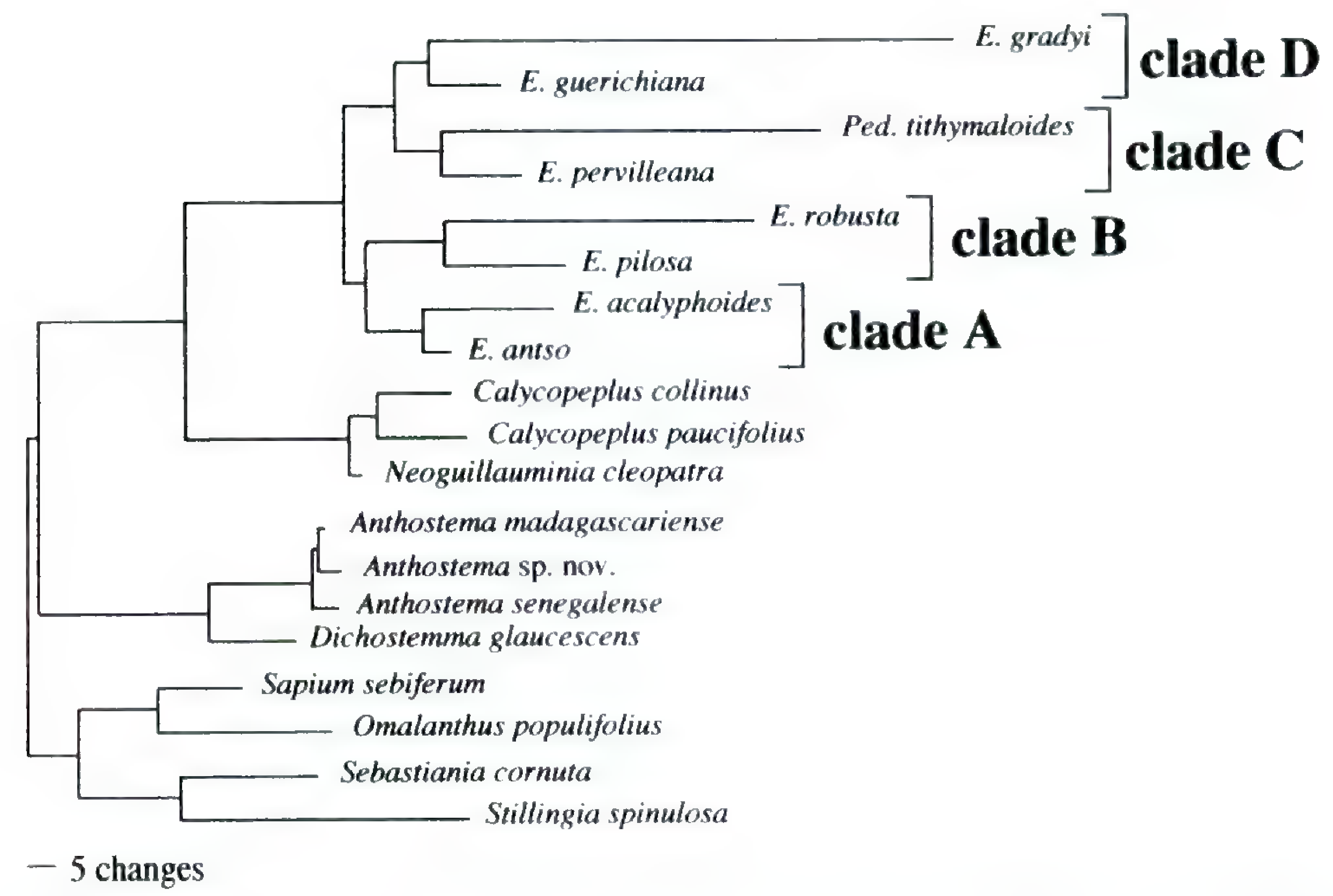

Figure 4. Phylogram of one of the equally most parsimonious trees resulting from the *ndh*F analysis, showing branch lengths within Euphorbieae. Only the species with the least and most changes are shown for each of the major clades of subtribe Euphorbiinae. Individual phylograms of clades A–D are given in Steinmann (2001). *E.* = *Euphorbia*, *Ped.* = *Pedilanthus*.

Cubanthus. *Cubanthus* was initially described as a section of *Pedilanthus*, but as noted by Millspaugh (1913) and confirmed by Dressler (1957), these two groups do not appear closely related. Although *Cubanthus* was not available for this study, *Euphorbia gymnonota* Urb. and *E. punicea* Sw. were included (clade C, Figs. 9, 11). Like members of *Cubanthus*, these two species possess involucral glands that are partially situated on the outside wall of the involucre in contrast to the rim of the involucre, as is generally the situation in *Euphorbia*. Based on this shared feature, an overall similarity in habit, and an allopatric distribution, *Cubanthus* is presumably closely related to these taxa and probably would associate with them in a molecular analysis.

Euphorbia *subg.* Trichadenia. Pax (1921) first proposed this taxon as a section of *Euphorbia*, but a decade later he synonymized it with *Euphorbia* sect. *Tithymalus* Roeper, without elaborating on which group within section *Tithymalus* he believed that it belonged. Carter (1985) resurrected *E.* sect. *Trichadenia* Pax as a subgenus and proposed two sections: sect. *Somalica* S. Carter (inflorescences umbellate and unbranched, with small deciduous bracts) and sect. *Trichadenia* (inflorescences branching, with large persistent bracts). Later she removed her section *Somalica* from *Euphorbia* subg. *Trichadenia* and placed it in subgenus *Lyciopsis* (Carter, 1988a). Although *E.* subg. *Trichadenia* (Pax) S. Carter is now generally accepted, its exact rank and placement are disputed. Based presumably on the fact that many species possess a pseudoumbellate inflorescence, Gilbert (1987, 1990), for example, preferred to treat it within *E.* subg. *Esula*.

Various species referred to *Euphorbia* subg. *Trichadenia* by Pax, Carter, and Gilbert were included in this study: *Euphorbia trichadenia* Pax, *E. goetzei* Pax, *E. platycephala* Pax, *E. grantii* Oliv., and *E. omariana* M. G. Gilbert. With the exception of *E. goetzei*, which falls out in clade D as related to *E. pirottae* N. Terrac. (Figs. 12, 14), the members of subgenus *Trichadenia* are supported to be closely related and belong to clade A (Figs. 5, 6). However, they do not form a monophyletic group. Instead, they belong to a group together with *Euphorbia* sects. *Dactylanthes* (Haw.) A. Berger, *Medusea* (Haw.) Baill., *Meleuphorbia* A. Berger, *Treisia* (Haw.) Baill., and *Anthacantha* (Lem.) A. Berger. These sections, which lack a current subgeneric placement, all contain tuberculate-stemmed South African succulents, many of which also possess glandular involucral processes. Their various characteristics are as follows: *E.* sect. *Anthacantha* (leaf-reduced stems, the inflorescences axillary with the cyathia borne at the tips of persistent, spiny peduncles; representative: *E. atrispina* N. E. Br.); *E.* sect. *Dactylanthes* (leaf-reduced, highly branched, short stems, the involucral glands with long, fingerlike divisions and curved lip at the base; representative: *E. globosa* (Haw.) Sims); *E.* sect. *Treisia* (leafy stems and three conspicuous bracts just below the cyathium; representative: *E. clava*

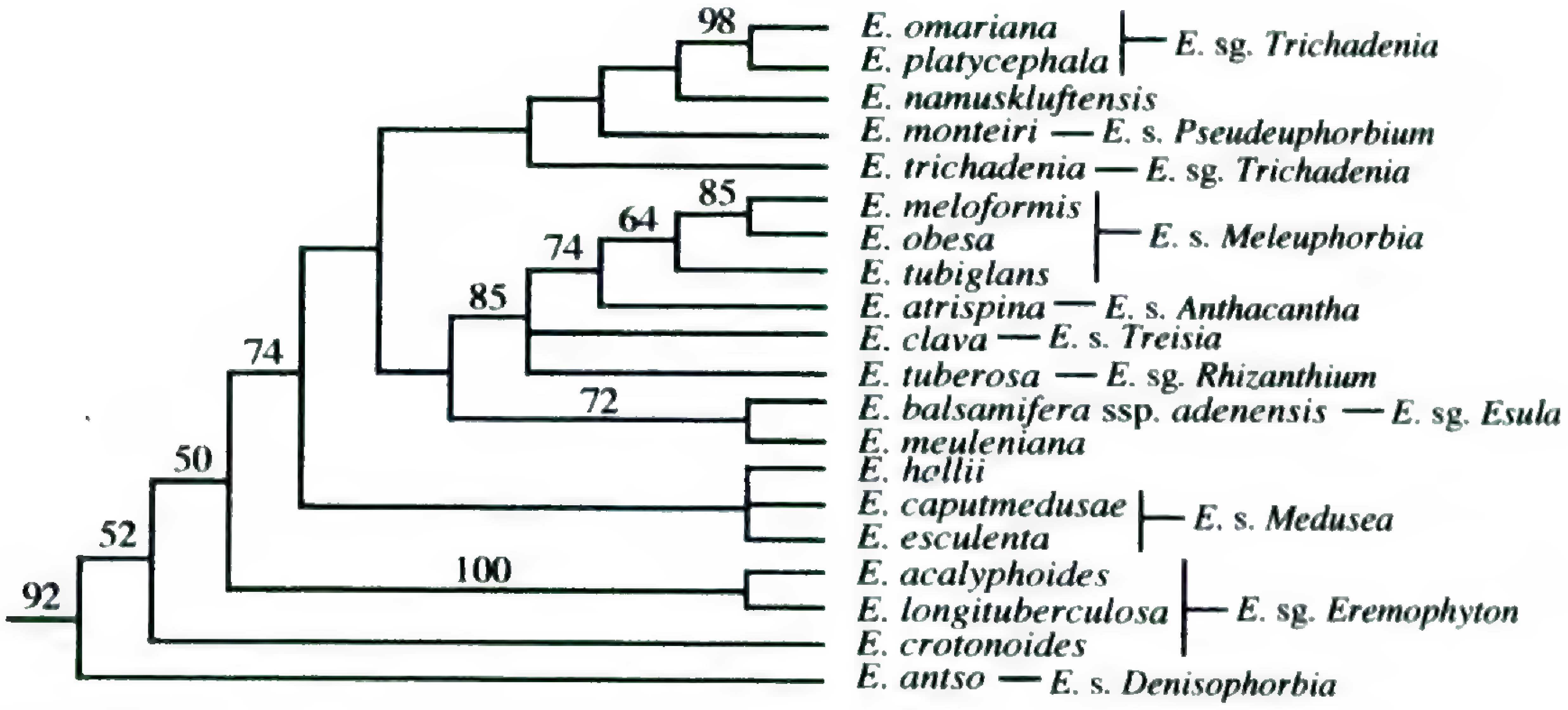

Figure 5. Euphorbiinae clade A, strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, s. = section, sg. = subgenus, ssp. = subspecies.

Jacq.); *E.* sect. *Medusea* (main stem normally partly sunken in the ground and with few to many secondary branches crowning and radiating from the apex; representatives: *E. caputmedusae* L. and *E. esculenta* Marloth); *E.* sect. *Meleuphorbia* (little-branched to unbranched aboveground stems that are frequently subglobose and with distinct angles; representatives: *E. tubiglans* Marloth ex R. A. Dyer, *E. obesa* Hook. f., and *E. meloformis* Aiton). The close relationship between the species of subgenus *Trichadenia* and these taxa is not surprising and was predicted by Gilbert (1987), who noted that there does not appear to be any important discontinuity between these groups. Also closely allied are *E. tuberosa* L., the type of *E.* subg. *Rhizanthium*; *E. monteiri* Hook. f., the type of *E.* sect. *Pseudeuphorbium* (Pax) A. Berger; and *E. lignosa* Marloth, the type of *E.* subg. *Lyciopsis* (Boiss.) L. C. Wheeler sect. *Lignosae* Pax & K. Hoffm.

Euphorbia *subg.* Rhizanthium. This taxon was initially proposed by Boissier (1862) as a section of *Euphorbia* to accommodate various geophytes from India and South Africa. Boissier (1862) treated another geophyte, *Euphorbia sessiliflora* Roxb. from Burma (not included here), in his *E.* sect. *Caulanthium* Boiss. Wheeler (1943) combined these two sections under the name *Rhizanthium* and elevated its rank to subgenus within *Euphorbia*. Gilbert (1987) provided a detailed overview of the group, concluding that subgenus *Rhizanthium*, as currently circumscribed, is a heterogeneous assemblage of many unrelated species. This study vindicates his contention, and members of this taxon belong to various unrelated groups in clades A and C (see Figs. 5, 6, 10, 11).

A number of species in *Euphorbia* subg. *Rhizanthium* were included here. Although *Euphorbia sessiliflora*, the sole member of Boissier's *Euphorbia* sect. *Caulanthium*, was not available for inclusion, the later-described and apparently closely related *E. panchganiensis* Blatt. & McCann and *E. meenae* S. Carter were represented. Both of these Indian geophytes are nested within the spine-shield succulents of *E.* subg. *Euphorbia*. *Euphorbia tuberosa*,

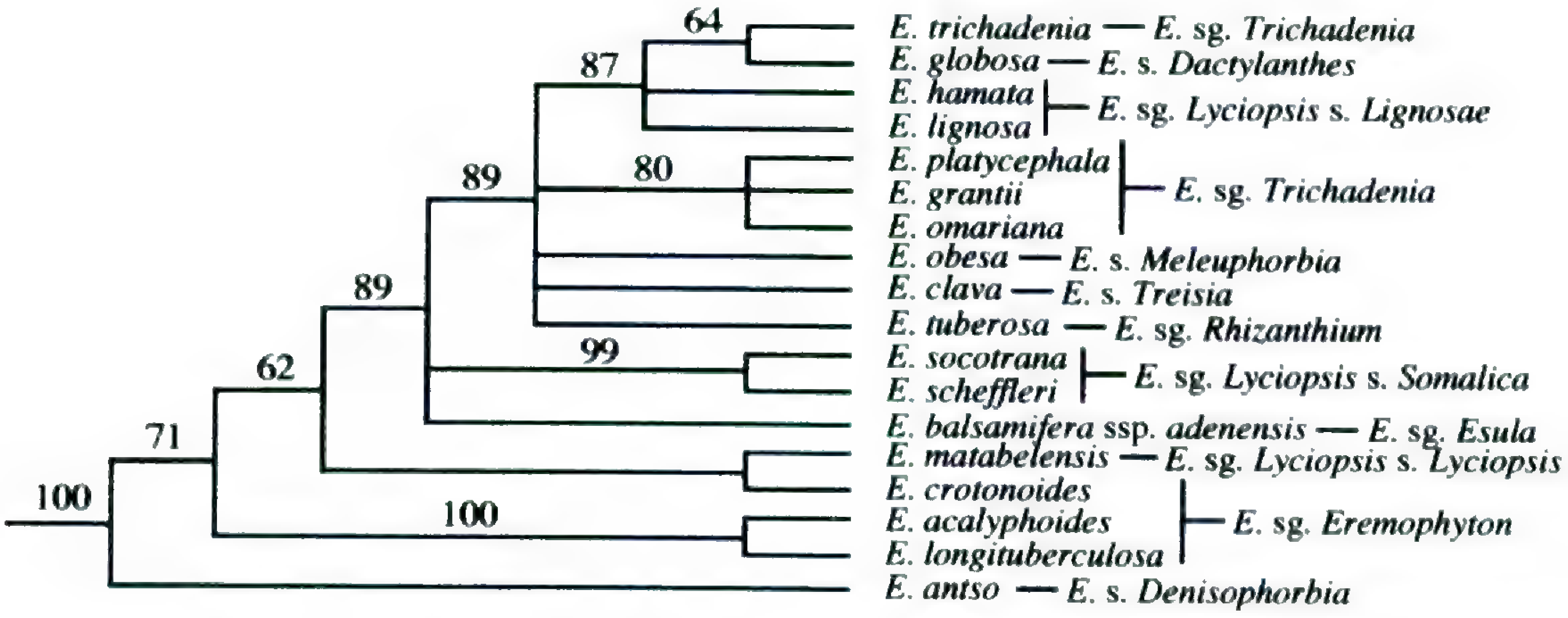

Figure 6. Euphorbiinae clade A, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, s. = section, sg. = subgenus, ssp. = subspecies.

the type of subgenus *Rhizanthium*, is not closely related to the Indian species, but instead is related to a group of South African taxa currently recognized as *E.* subg. *Trichadenia* (clade A, Figs. 5, 6; see discussion above). Despite not truly being geophytes, *E. longituberculosa* Boiss. and *E. pirottae* were placed here by Pax and Hoffmann (1931). The first species is not closely related to any of the above members, but instead its position is near *E. acalyphoides* Hochst. ex Boiss. in *E.* subg. *Eremophyton* sect. *Pseudacalypha* Boiss. in clade A (Figs. 5, 6), where it was placed by Carter (1988a). The second species also shows no affinities with any of the above members and comes out related to *Euphorbia goetzei* within clade D (Figs. 12, 14). *Euphorbia primulifolia* Baker, a Madagascan species treated in subgenus *Rhizanthium* by Denis (1921) and in *E.* subg. *Lacanthis* by Gilbert (1987), belongs with other Madagascan species currently placed in subgenus *Lacanthis* (clade C, Fig. 10).

Euphorbia *subg.* Lyciopsis. When first described as a section (Boissier, 1862), this taxon contained only *Euphorbia cuneata* Vahl, a spinescent shrub from Africa with fasciculate leaves. The section was compared with *E.* sect. *Tirucalli* Boiss. in gland characters but distinguished by the fasciculate leaves and non-succulent stems. Pax and Hoffmann (1931) expanded section *Lyciopsis* Boiss. to include three subsections: subsect. *Lyciopsis* (as *Eulyciopsis*), subsect. *Espinosae* (Pax & K. Hoffm.) Pax & K. Hoffm., and subsect. *Lignosae* (Pax & K. Hoffm.) Pax & K. Hoffm. The latter two were based on sections proposed a decade earlier (Pax & Hoffmann in Pax, 1921). Wheeler (1943) followed Pax's circumscription and made changes only in rank when elevating this taxon to subgenus. Carter (1988a) expanded it to include an additional section, *E.* sect. *Somalica*, a group erected by her to accommodate about 10 east African species with woody semisucculent branches, small scarious deciduous bracts, crenulate or pectinate involucral glands, and large, often ornamented capsules (Carter, 1988b); *E.* sect. *Somalica* was previously placed in *E.* subg. *Trichadenia* (Carter, 1985).

Members of all four currently recognized sections of *Euphorbia* subg. *Lyciopsis* were included in this analysis. The results suggest that the subgenus is polyphyletic, and its component sections represent four distinct groups. In both molecular analyses, *E. espinosa* Pax and *E. guerichiana* Pax form a well-supported lineage (bs 97% in ITS, 100% in *ndh*F) in the early diverging portion of clade D (Figs. 12, 14). They are far removed from the remainder of the sections of subgenus *Lyciopsis*, all of which belong to clade A (Fig. 6). Due to problems obtaining ITS sequences, the other species of this subgenus were included only in the *ndh*F analysis. Both *E. lignosa* and *E. hamata* (Haw.) Sweet, members of subgenus *Lyciopsis* sect. *Lignosae*, are placed in a well-supported clade (bs 87%) together with *E. trichadenia* and *E. globosa*. Their relationship here is not unexpected; Pax and Hoffmann (in Pax, 1921), when first describing this section, noted that the appendages of *E. lignosa* were similar to those of species in *E.* sect. *Dactylanthes*, of which *E. globosa* is a member.

The only species of *Euphorbia* subg. *Lyciopsis* sect. *Lyciopsis* that was included in this study is *E. matabelensis*. It comes out as an early diverging member of clade A, sister to *E. crotonoides* Boiss. However, this relationship should be viewed with reservation because there is little morphological similarity between these two species and no bootstrap support for this grouping.

The final section, *Euphorbia* subg. *Lyciopsis* sect. *Somalica*, was represented in this study by two species, *E. scheffleri* Pax and *E. socotrana* Balf. f. These two form a well-supported group (bs 99% in *ndh*F, Fig. 6) in a subclade containing *E. balsamifera* Aiton and various other *Euphorbia*. *Euphorbia balsamifera* is vegetatively similar to species of subgenus *Lyciopsis* sect. *Somalica*, so the suggestion that they have arisen from common ancestry is reasonable.

Euphorbia *subg.* Esula. This subgenus largely corresponds to Boissier's *Euphorbia* sect. *Tithymalus*. Wheeler (1943), when implementing his system of subgenera, resurrected the application of *E.* subg. *Esula* for this assemblage. Its current use corresponds to the circumscriptions of these authors with some subsequent modifications. For example, *E. ipecacuanhae* L., the type of Boissier's section *Tithymalus* subsect. *Ipecacuanhae* Boiss., has been transferred to *E.* subg. *Agaloma*, and *Tithymalus* subsect. *Inundatae* has been proposed to accommodate the remainder of the species treated in this subsection (Webster, 1967). In addition, *E.* sect. *Tithymalus* subsect. *Crotonopsideae* Boiss. was removed by Radcliffe-Smith (1974) and placed in subgenus *Cystidospermum* (Prokh.) Prokh. (see discussion under *Euphorbia* subg. *Eremophyton*). As employed in the discussion below, many of Boissier's subsections are elevated to the rank of section when *E.* sect. *Tithymalus* is treated as *E.* subg. *Esula*.

With as many as 500 species, this is the largest subgenus currently recognized within *Euphorbia*. It probably is also the most taxonomically difficult.

The greatest diversity is in northern temperate regions. Plants are mostly perennial herbs, but a variety of growth forms exist from diminutive annuals to shrubs or rarely small trees. The majority of *E.* subg. *Esula* possess alternate lower leaves and a well-developed pseudoumbellate inflorescence in which the stem terminates in a whorl of leaves and a fascicle of three to many branches with opposite leaves and dichotomous branching; cyathia are situated in the axils of these upper leaves. The involucral glands lack appendages and are often truncate or bicornute. Exstipulate leaves also characterize this group, but some members currently placed here possess stipules, e.g., the species of subgenus *Esula* sect. *Adenorima* (Raf.) G. L. Webster and section *Tithymalus* subsect. *Inundatae.*

About 45 species of *Euphorbia* subg. *Esula,* from the majority of Boissier's subsections, were included in this study. Although most of Boissier's subsections were sampled, not enough members from each were included to make any definitive inferences concerning their monophyly. Still, a number of conclusions can be reached.

Euphorbia ipecacuanhae, the basis of Boissier's section *Tithymalus* subsect. *Ipecacuanhae,* was indeed supported as being unrelated to other members of this subsection (currently treated as *E.* subg. *Esula* sect. *Tithymalus* subsect. *Inundatae)* as well as unrelated to other members of subgenus *Esula*; thus, its removal by Webster (1967) is justified. *Euphorbia ipecacuanhae* belongs with members of subgenus *Agaloma* in clade D (see Fig. 13). Also justified is Radcliffe-Smith's placement of section *Tithymalus* subsect. *Crotonopsideae* within *Euphorbia* subg. *Cystidospermum* (see discussion under *E.* subg. *Eremophyton*).

Euphorbia subg. *Esula* sect. *Tithymalus* subsect. *Inundatae* was represented by three South American species: *E. papillosa* A. St.-Hil., *E. stenophylla* (Klotzsch & Garcke) Boiss., and *E. thinophila* Phil. These do not demonstrate any close relationship to other members of subgenus *Esula.* Instead, the molecular evidence supports that they are related to *E. peperomioides* Boiss. of section *Nummulariopsis* Boiss. and *E. germainii* Phil. of section *Portulacastrum* Boiss. Together these form a monophyletic group in clade C (see Fig. 9).

Euphorbia subg. *Esula* sect. *Balsamis* Webb. & Berthel., a taxon corresponding to Boissier's section *Tithymalus* subsect. *Pachycladae,* is clearly polyphyletic (Figs. 5–9, 11). This is not surprising, considering that the only features uniting its members are their shrubby habit together with branches that are leafy only toward the tips but leafless with prominent leaf scars proximally. *Euphorbia balsamifera* subsp. *adenensis* (see Figs. 5, 6) does not appear closely related to any other species of subgenus *Esula* sect. *Balsamis* sampled here. Instead, it belongs to clade A and based on the ITS results (Fig. 5), it has its affinity with *E. meuleniana* O. Schwartz from Yemen, a vegetatively similar species. *Euphorbia plumerioides* Teijsm. ex Hassk., also referred to this group by Boissier, shows no close relationship to *E. balsamifera* but instead belongs to clade C (Fig. 9). *Euphorbia plumerioides* is a member of a group of about eight species occurring in Australia, Malesia, and Melanesia (Foster, 1994). In this analysis, the Hawaiian species, *E. haeleeleana* D. R. Herbst, is suggested to belong to this group. Also related is *E. boöphthona* C. A. Gardner, an herbaceous plant from Australia previously treated in subgenus *Eremophyton.* Both *E. balsamifera* and members of the *E. plumerioides* group differ from typical members of subgenus *Esula* by lacking the characteristic pseudoumbellate inflorescence described above. A third group of species sampled from subgenus *Esula* sect. *Balsamis, E. dendroides* L., *E. longifolia* Lam., *E. regis-jubae* Webb. & Berthel., and *E. atropurpurea* Brouss. ex Willd., are demonstrated by the molecular evidence to be related to typical members of the north temperate group of subgenus *Esula* discussed below (see Figs. 7, 8), although collectively these do not form a monophyletic group.

Another group that does not appear related to the remainder of *Euphorbia* subg. *Esula* is its section *Adenorima.* This taxon corresponds to Boissier's section *Tithymalus* subsect. *Laurifoliae*; another synonym is the genus *Euphorbiodendron* Millsp. As the last name suggests, the ca. 20 species composing *E.* subg. *Esula* sect. *Adenorima* are usually trees. They occur primarily in tropical forests from Mexico to northern South America and the Caribbean and possess the pseudoumbellate inflorescence structure typical of subgenus *Esula.* It is for this reason that they traditionally have been placed here. A number of species presently referable to subgenus *Esula* sect. *Adenorima* were included in this study: *E. punicea* Sw., *E. cestrifolia* HBK, *E. laurifolia* Juss., *E. elata* Brandegee, *E. tanquahuete* Sessé & Mociño, *E. calyculata* HBK, and *E. gymnonota* Urb. (Figs. 9, 11). These taxa do not appear closely related to the core *Esula* group discussed below, and the two groups are in separate major clades of Euphorbiinae, clades C and B, respectively. In addition, the species of subgenus *Esula* sect. *Adenorima* do not form a monophyletic group, but instead appear to represent an ancestral New World grade from which various other groups of *Eu-*

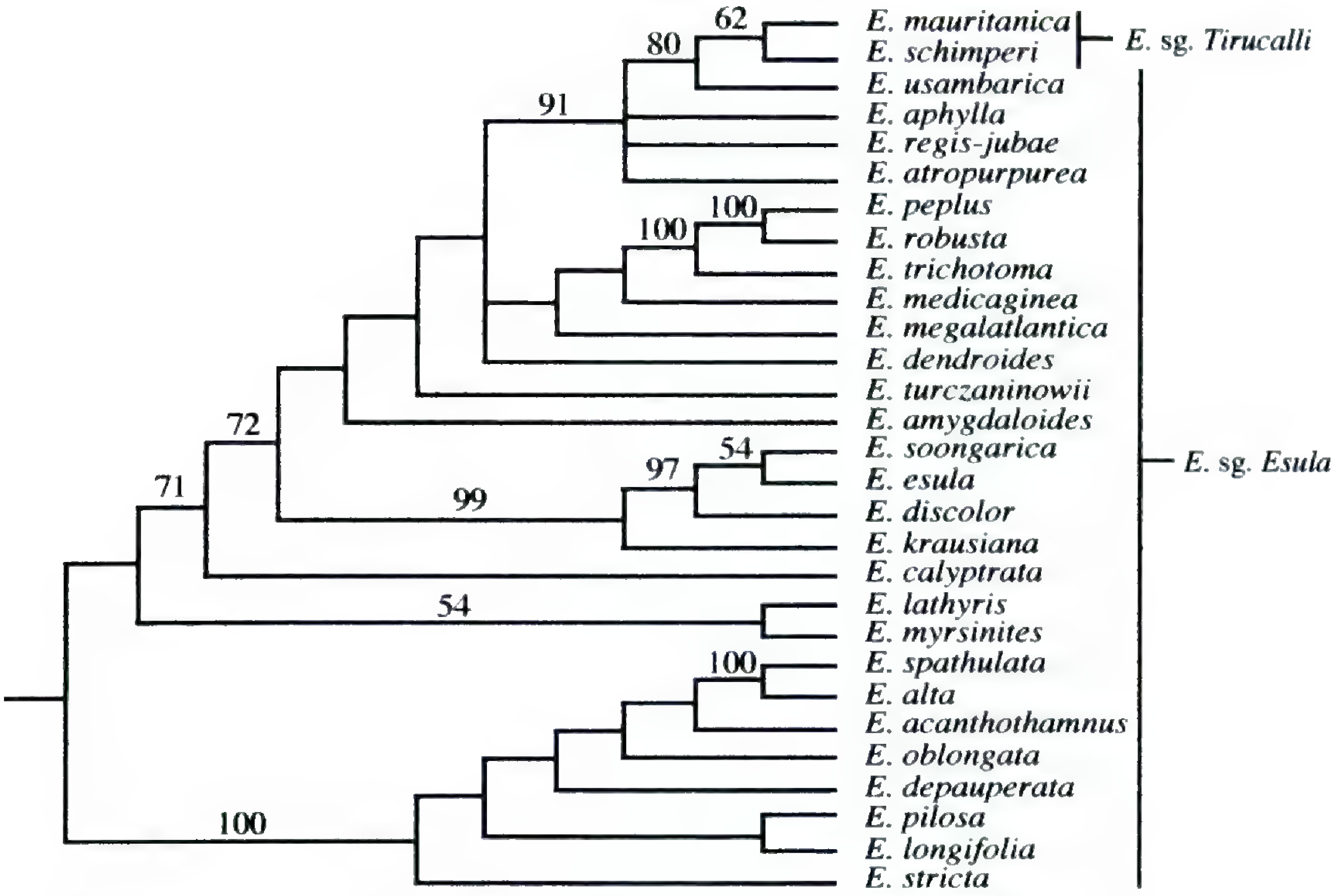

Figure 7. Euphorbiinae clade B, strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, sg. = subgenus.

phorbia have evolved. Dressler (1957) suggested that this taxon includes the most primitive members of the genus. Although that assumption is not strongly supported here, the species do represent some of the earliest diverging taxa in clade C and possess many traits that appear primitive for the genus.

In both the ITS and *ndh*F analyses, the remaining species of *Euphorbia* subg. *Esula* sampled come out together (see Figs. 7, 8). This group corresponds to the following subsections of Boissier's section *Tithymalus*: subsect. *Decussatae* Boiss., subsect. *Oppositifoliae* Boiss., subsect. *Carunculares* Boiss., subsect. *Galarrhaei* Boiss., subsect. *Esulae* Boiss., and subsect. *Myrsiniteae* Boiss. They form a well-supported, monophyletic assemblage (bs 86% in *ndh*F) only after the inclusion of the third group of species discussed above in subgenus *Esula* sect. *Balsamis* and the inclusion of *E. schimperi* Presl and *E. mauritanica* L. The latter two species have been placed in *E.* subg. *Tirucalli*, but it should be emphasized that their association with *E. tirucalli* L. and relatives is based primarily on gross morphology; the possession of pseudoumbellate inflorescences and the lack of stipules supports their placement in subgenus *Esula*, as the molecular data here strongly suggest.

Collectively the taxa mentioned in the previous paragraph compose clade B and correspond broadly to the temperate, Northern Hemisphere group of *Euphorbia* subg. *Esula*. The presence of *Euphorbia* in temperate regions is almost entirely the result of the radiation of this lineage, and very few other species of *Euphorbia* are found in such areas. Although the great majority of this group are restricted to temperate, Northern Hemisphere environments or high-elevation montane tropical regions, this is not a strict characterization. *Euphorbia mauritanica* and relatives are found in arid tropical and subtropical regions; *E. dendroides*, *E. longifolia*, *E. regis-jubae*, and *E. atropurpurea* occur in subtropical vegetation on the Canary Islands; and *E. trichotoma* inhabits beaches in the New World tropics.

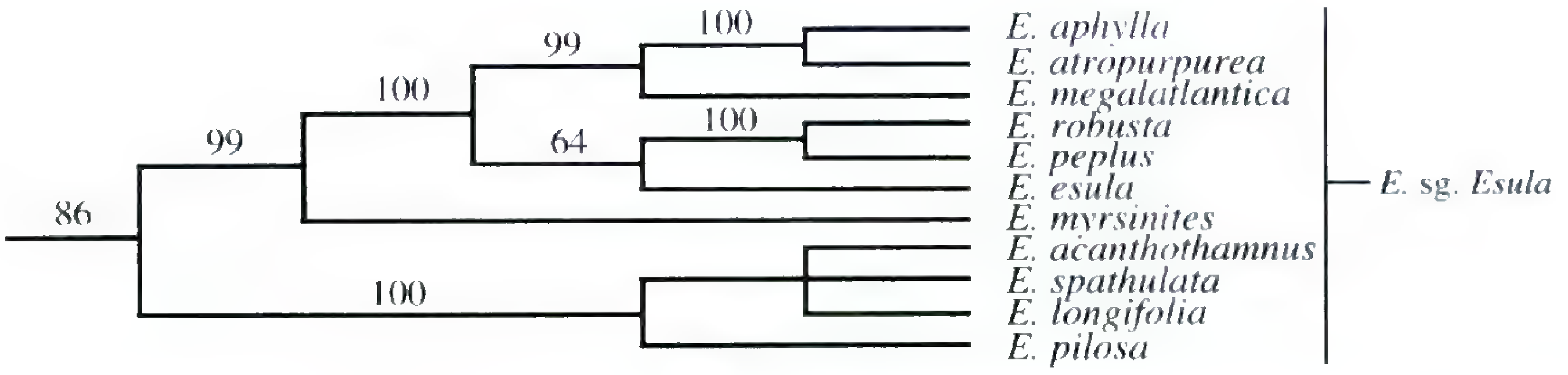

Figure 8. Euphorbiinae clade B, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, sg. = subgenus.

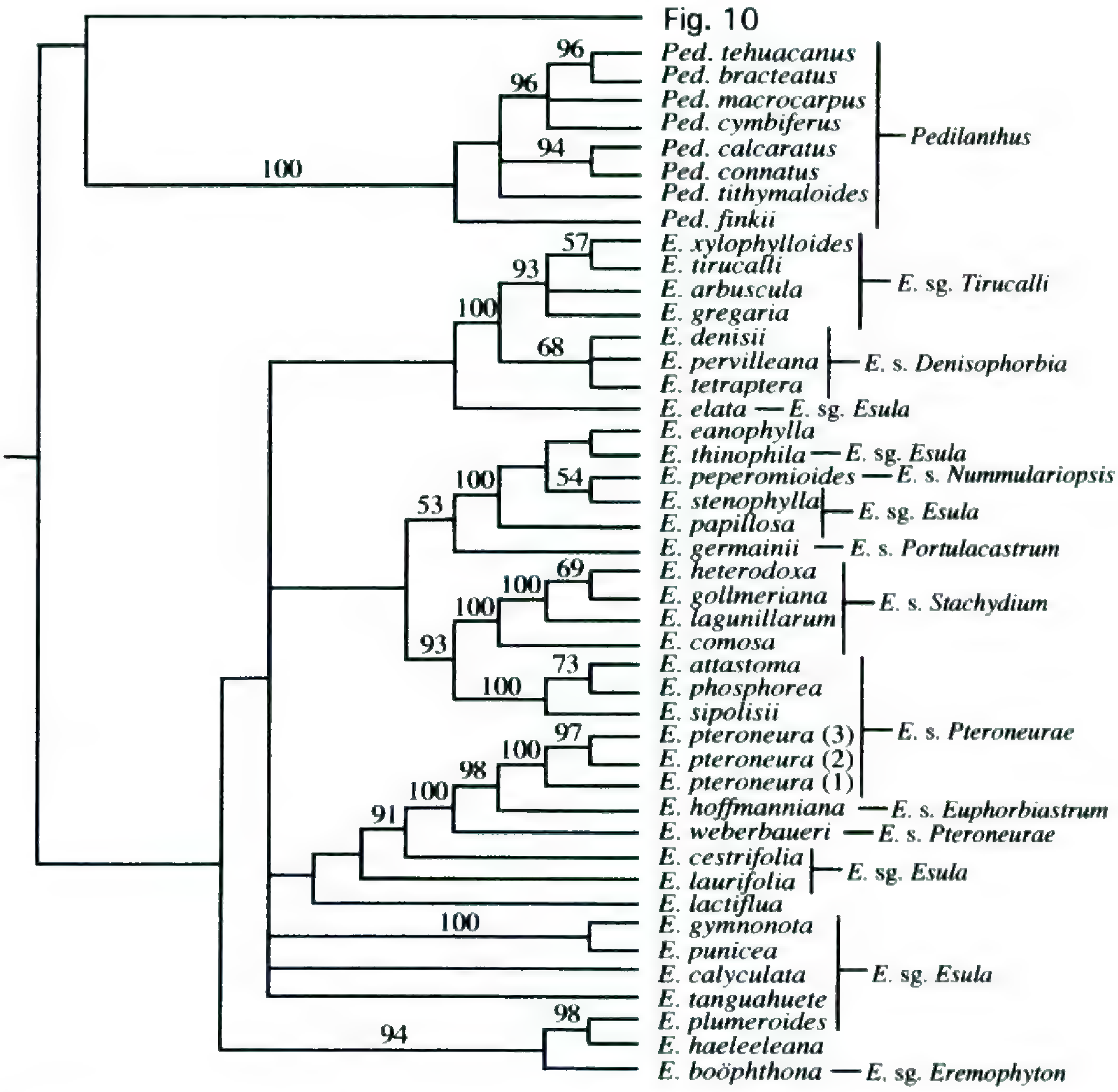

Figure 9. Euphorbiinae clade C (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *Ped.* = *Pedilanthus*, s. = section, sg. = subgenus, ssp. = subspecies.

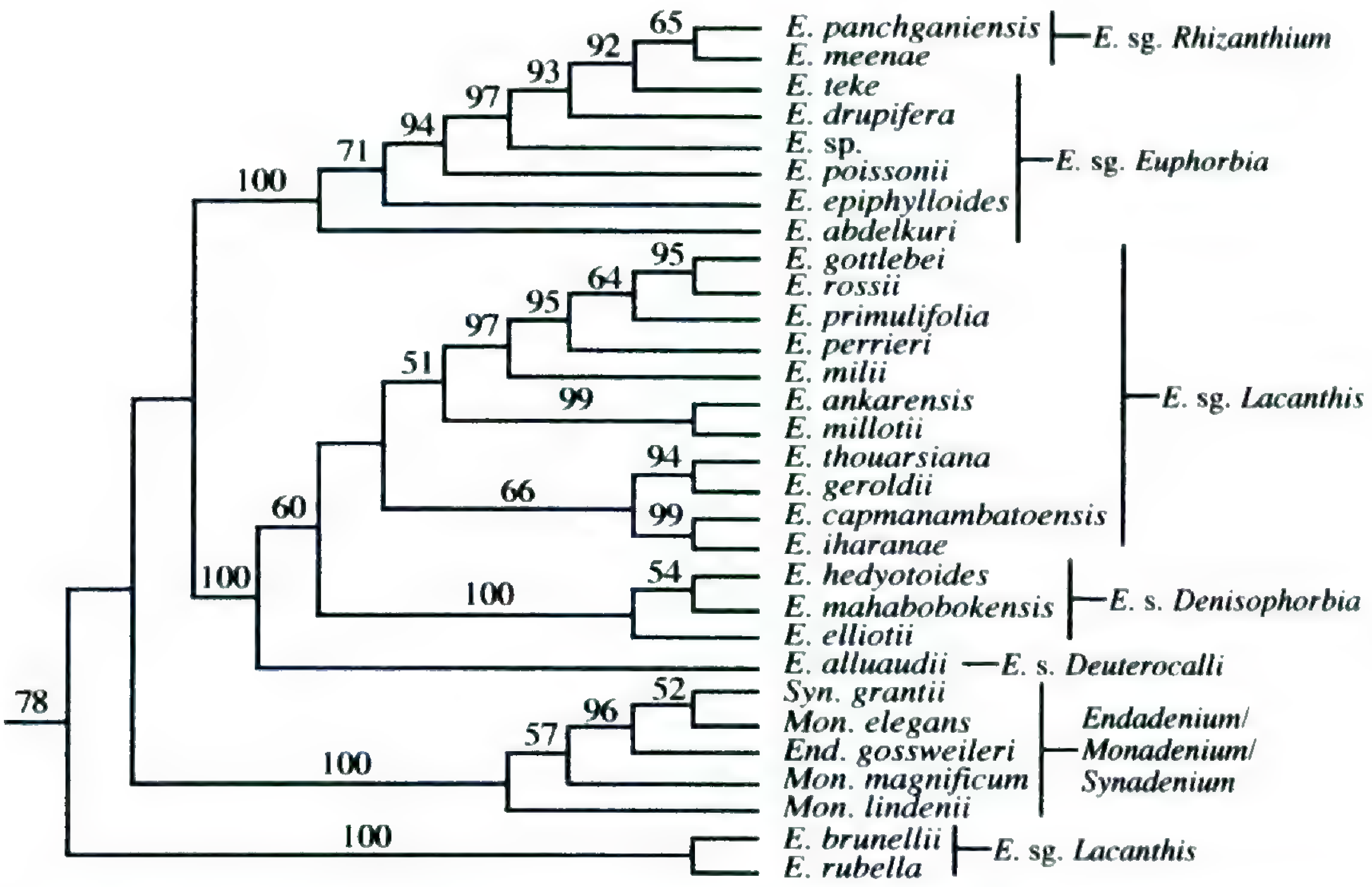

Figure 10. Euphorbiinae clade C (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *End.* = *Endadenium*, *Mon.* = *Monadenium*, *Syn.* = *Synadenium*, s. = section, sg. = subgenus.

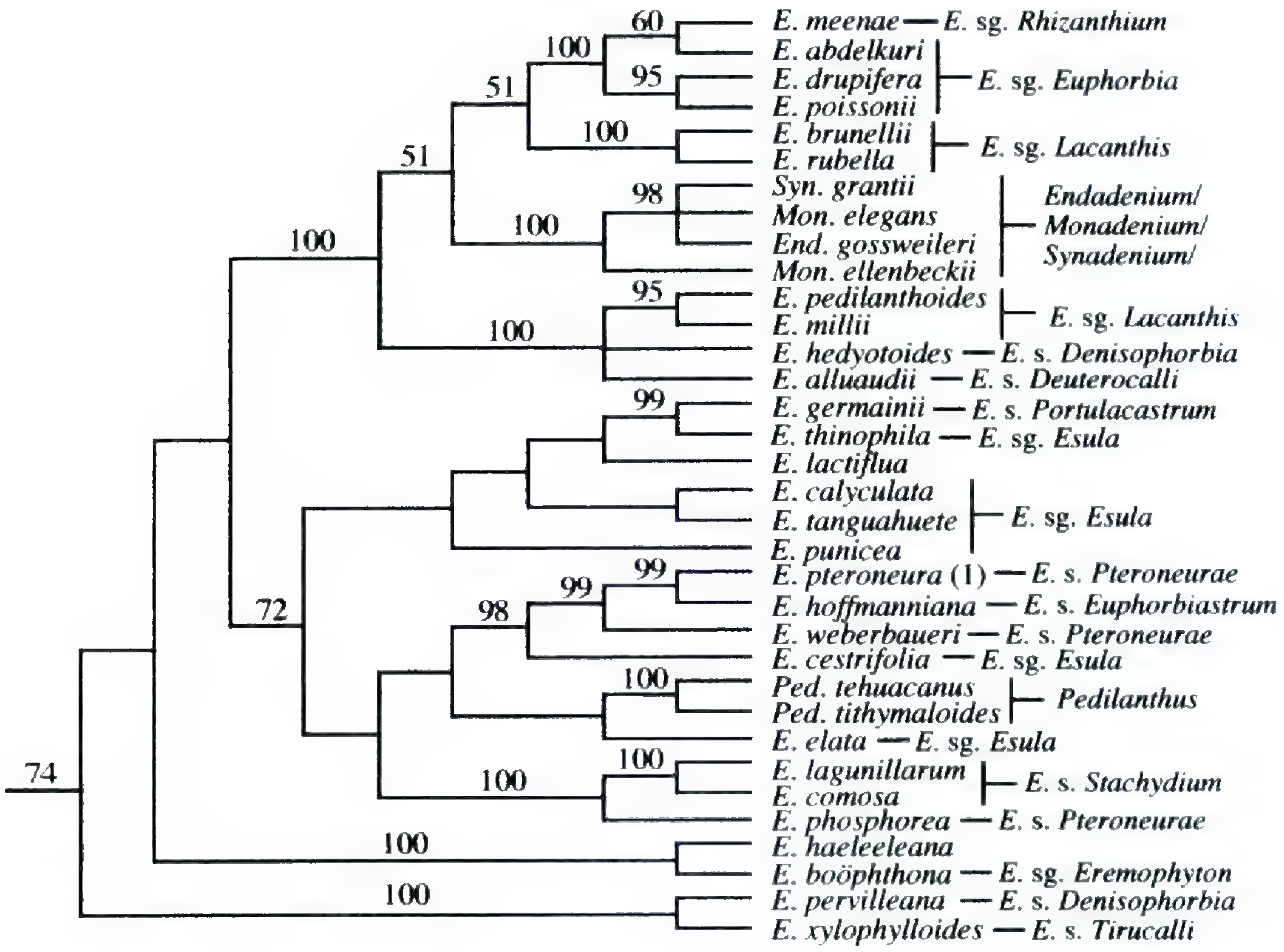

Figure 11. Euphorbiinae clade C, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *End.* *Endadenium*, *Mon.* = *Monadenium*, *Ped.* = *Pedilanthus*, *Syn.* = *Synadenium*, s. = section, sg. = subgenus.

At least from the limited sample examined in this study, the primary division within the restricted circumscription of *Euphorbia* subg. *Esula*, discussed in the previous two paragraphs, is between those species that possess tuberculate ovaries and those species whose ovaries are smooth. It remains to be seen whether this distinction will withstand an increase in sampling. If so, this would have important taxonomic implications because many of Boissier's subsections contain both tuberculate- and smooth-ovaried species.

It is worth emphasizing that the occurrence of a pseudoumbellate inflorescence in all of the major lineages of *Euphorbia* suggests this is a symplesiomorphic feature that was present before the differentiation of subtribe Euphorbiinae. The structure bears some resemblance to the inflorescence of *Neoguillauminia* and may be homologous. Therefore, the possession of this type of inflorescence should not be viewed as the defining characteristic of *E.* subg. *Esula*. Instead, it is the combination of a pseudumbellate inflorescence together with exstipulate leaves that better characterizes the core subgenus *Esula* group, as represented by clade B.

Euphorbia *sect.* Nummulariopsis. *Euphorbia peperomioides* and the very similar *E. paranensis* Dusén (the latter not included) are the only two species belonging to *E.* sect. *Nummulariopsis*. Both are prostrate Brazilian perennial herbs with opposite, asymmetrical leaves and elongate, glandular stipules. These features together with axillary, 4-glanded involucres are reminiscent of *Chamaesyce*, to which Wheeler (1943) believed that this section belonged. Webster (1967) noted that *E. peperomioides* bordered *Chamaesyce*. In this analysis, *E. peperomioides* shows no affinity with *Chamaesyce*. It is instead related to *E. stenophylla*, a South American member of subgenus *Esula* sect. *Tithymalus* subsect. *Inundatae* (Fig. 9). Although in habit *E. peperomioides* and *E. paranensis* differ greatly from other members of this subsection, a close relationship is suggested by the common possession of subulate, sepal-like lobes below the pistillate flowers, a feature otherwise very rare in subtribe Euphorbiinae.

Euphorbia *sect.* Portulacastrum. Two species, *Euphorbia germainii* and *E. pentlandii* Boiss. (the latter not included), are contained in this section. Both are South American annuals with cleft involucral appendages. Based on the presence of these involucral appendages, section *Portulacastrum* has been placed in *E.* subg. *Agaloma*, e.g., Wheeler (1943). However, according to the molecular data, at least *E. germainii* does not fall out as related to the core *Agaloma* group. Instead, it nests within South American members of subgenus *Esula* sect. *Tithymalus* subsect. *Inundatae* in clade C (Fig. 9). This placement is anomalous, and *E. germainii* and

E. pentlandii are morphologically incongruous there because they possess well-developed involucral appendages and lack the characteristic sepal-like lobes below the pistillate flowers of the subsection *Inundatae*.

Euphorbia *sect.* Denisophorbia. This is a small group of approximately 20 species of leafy trees and shrubs, mostly confined to Madagascar. It was first proposed as a subsection of *Euphorbia* sect. *Euphorbia* by Leandri (1957). Croizat (1972) elevated the group to the rank of section. As mentioned by Leandri (1957), section *Denisophorbia* is difficult to define. The leaves are entire and alternate to spirally arranged. The cyathia are relatively large, lack appendages, and are solitary or in terminal pseudoumbellate inflorescences. Seven species belonging to this group were included here: *Euphorbia antso* Denis, *E. denisii* Oudejans, *E. elliotii* Leandri, *E. hedyotoides* N. E. Br., *E. mahabobokensis* Rauh, *E. pervilleana* Baill., and *E. tetraptera* Baker.

These species do not form a monophyletic clade but instead come out as representing three separate groups. *Euphorbia antso* is the earliest diverging species in clade A (Figs. 5, 6) and shows no affinity with the other species of *E.* sect. *Denisophorbia* sampled here, all of which belong to clade C (Figs. 9–11). *Euphorbia denisii, E. pervilleana,* and *E. tetraptera* form a monophyletic group that is sister to *E. tirucalli* and relatives, currently treated in subgenus *Tirucalli*. Not closely related to this group are *E. elliotii, E. hedyotoides,* and *E. mahabobokensis*. These form a monophyletic clade sister to *E.* subg. *Lacanthis* proper.

Euphorbia sect. *Denisophorbia* was proposed to be the most primitive group in *Euphorbia* (Webster et al., 1982). In part, this may be correct because *Euphorbia antso* is the earliest diverging species of clade A and possesses many of the primitive features for the subtribe (see discussion below under origin and biogeography of Euphorbieae). Also, with regard to ITS and *ndh*F molecular evolution this species possesses the least amount of genetic divergence in relation to the outgroup taxa (see Figs. 3, 4).

Euphorbia *subg.* Tirucalli. The section *Tirucalli* Boiss. was proposed in *Euphorbia* to accommodate arid-adapted shrubs with long, slender, semi-succulent branches (Boissier, 1862). The leaves are reduced and the stem is green and photosynthetic. The section was elevated to subgenus by Carter (1985), and she later noted that it contains two well-defined groups (Carter, 1992a). The first group corresponds to *E. tirucalli* and relatives and is characterized by small scarious bracts, tightly congested inflorescences, and glandular stipules. The second group corresponds to species such as *E. mauritanica* and is characterized by leafy bracts, pseudoumbellate inflorescences, and a lack of stipules.

Various members of *Euphorbia* subg. *Tirucalli* were included in this analysis, and the two groups recognized by Carter do not appear closely related. Instead, their similarities in growth form appear to have resulted from convergent evolution. *Euphorbia tirucalli* and relatives (represented here by *E. arbuscula* Balf. f., *E. gregaria* Marloth, and *E. xylophylloides* Brongn. ex Lem.) come out in clade C as sister to a group of leafy shrubs from Madagascar that are currently treated in section *Denisophorbia* (Figs. 10, 11). The remainder of the species of subgenus *Tirucalli* (represented here by *E. mauritanica* and *E. schimperi*) are found nested within the north-temperate group of subgenus *Esula* in clade B (Fig. 7). The leafy bracts, pseudumbellate inflorescences, and lack of stipules of these latter plants substantiate this placement.

Euphorbia lactiflua Phil. ex Boiss., a shrub from the deserts of Chile and the only New World species referred to this group (Boissier, 1862), is not related to any other species of the subgenus (Figs. 9, 11). In fact, its initial placement by Boissier is in itself very peculiar because this species is a leafy, scarcely succulent shrub. *Euphorbia lactiflua* is taxonomically isolated and shows no close relationship with any other species of *Euphorbia*. In this analysis, its affinities are not determined with precision, but belongs to clade C, in a group of various Neotropical *Euphorbia*.

Euphorbia *sect.* Euphorbiastrum. This taxon was first erected as a genus by Klotzsch and Garcke (1860) to accommodate their new species, *Euphorbiastrum hoffmanniana* Klotzsch & Garcke. Boissier (1862) then reduced *Euphorbiastrum* Klotzsch & Garcke to a section of *Euphorbia*. Its most distinctive feature is that the involucres are solitary in the leaf axils and subtended by a condensed spiral of small, imbricate bracts. In this analysis, *Euphorbia hoffmanniana* (Klotzsch & Garcke) Boiss. occurs in clade C where it is related to *E. weberbaueri* Mansf. and *E. pteroneura* A. Berger in a well-supported group (bs 91% in ITS, 98% in *ndh*F) together with *E. cestrifolia* (Figs. 9, 11). According to the ITS evidence (Fig. 9), *E. laurifolia* is the basal member of this assemblage, but there is no bootstrap support for its placement.

Members of this group are morphologically quite different. *Euphorbia cestrifolia* and *E. hoffmanniana* are leafy shrubs; *E. weberbaueri* is a leaf-re-

duced, stem-succulent shrub; and *E. pteroneura* is a leafy, drought-deciduous herbaceous succulent. Despite their gross differences in habit, some features suggest relationships among these plants. For one, both *E. cestrifolia* and *E. weberbaueri* possess complex, well-developed glandular stipules. As well, in all taxa the cyathia are closely subtended and sometimes enclosed in a pair of bracts, the styles are entire or emarginate, and the seeds are similar in size and shape and possess a minute caruncle. The involucres of *E. weberbaueri* and *E. pteroneura* possess four glands while those of *E. cestrifolia* and *E. hoffmanniana* possess five glands.

Euphorbia pteroneura was the basis for *E.* sect. *Pteroneurae* A. Berger (1906). Other taxa have been placed in this section, e.g., *E. sipolisii* and *E. phosphorea*, but a close relationship between these and *E. pteroneura* is not supported here (Figs. 9, 11). Given the close affinity of *E. hoffmanniana* and *E. pteroneura*, section *Pteroneurae* is best reduced to synonymy under *E.* sect. *Euphorbiastrum.*

Euphorbia *sect.* Stachydium. This section is characterized by a congested, primarily monochasial inflorescence on which the pairs of bracts are closely imbricate and fold over to obscure the involucres within. There are about five species in South America and one species, *Euphorbia phylloclada* Boiss., in Namibia. Boissier (1862), who first described *E.* sect. *Stachydium* Boiss., recognized two subsections: subsect. *Americanae* Boiss. (for the American species) and subsect. *Capensis* Boiss. (for *E. phylloclada*). Five species were included here: *E. comosa* Vell., *E. gollmeriana* Klotzsch ex Boiss., *E. heterodoxa* Müll. Arg., *E. lagunillarum* Croizat, and *E. phylloclada.* In this analysis, the two subsections are placed in different major clades of Euphorbiinae (clades C and D, respectively), and a close relationship between them is not supported. The similarity between the two subsections is due mostly to the unusual architecture of the inflorescence. Pax (1921) treated *Euphorbia phylloclada* as a member of *E.* sect. *Pseudacalypha*, based presumably on the axillary cyathia, but there is no affinity between this species and other members of *Pseudacalypha* either.

Based on the possession of involucral appendages, *Euphorbia* sect. *Stachydium* has been suggested to belong to subgenus *Agaloma* (Wheeler, 1943). However, only *E. phylloclada* occurs within this group (see discussion under subg. *Agaloma*). The South American species are members of clade C (Figs. 9, 11) and form a well-supported group (bs 93% in ITS, 100% in *ndh*F) that is sister to the *E. phosphorea* complex, a small assemblage of leafless, stem-succulents from eastern Brazil. Beyond its association with the *E. phosphorea* complex, the relationship of section *Stachydium* to other members of the genus is obscure, although the *ndh*F results suggest that it belongs to a weakly supported clade of various Neotropical taxa, including *Pedilanthus* and subgenus *Esula* sect. *Adenorima.*

Euphorbia *subg.* Euphorbia. Following the most recent modifications in *Euphorbia* classification (Gilbert, 1987; Carter, 1988a), the subgenus *Euphorbia* is restricted to about 250 Old World stem succulents in which the base of each leaf is surrounded by a callous pad, termed a spine-shield, bearing a pair of spiny outgrowths and stipules modified into spines. It corresponds to Haworth's (1812) and Klotzsch and Garcke's (1859, 1860) restricted genus *Euphorbia.* Boissier treated these species together with *E. milii* Des Moul. (= *E. splendens* Boj. ex Hook.) under his *E.* sect. *Diacanthium* Boiss. Although Bentham's (1880) and Pax and Hoffmann's (1931) classifications recognized section *Diacanthium* in the same sense as Boissier, it was reduced to a subsection of section *Euphorbium* Boiss., a taxon these authors used to accommodate essentially all of the succulent *Euphorbia* species. Wheeler (1943) followed Bentham's and Pax and Hoffmann's circumscription but under the misapplied name *E.* subg. *Tithymalus*; the name *Tithymalus* has otherwise usually been applied to the north temperate members of *E.* subg. *Esula.* Webster (1967) essentially followed Wheeler's classification but correctly applied the name *E.* subg. *Euphorbia* to this assemblage.

In both the *ndh*F and ITS analyses, *Euphorbia* subg. *Euphorbia* belongs to a well-supported clade (bs 78% in ITS, 100% in *ndh*F) together with subgenus *Lacanthis* and the *Synadenium* alliance (Figs. 10, 11). Within this clade, all of subgenus *Euphorbia* sampled form a monophyletic group, but only after the inclusion of a few additional taxa. *Elaeophorbia*, an African group of four species with drupaceous fruits, has been recognized as a genus by some (e.g., Carter, 1988a) and a section by others (e.g., Webster, 1967). It was represented in this study by *E. drupifera* Thonn. and well supported (bs 100% in both analyses) to be nested within subgenus *Euphorbia* (Figs. 10, 11). In addition, *E. panchganiensis* and *E. meenae* are also strongly supported (bs 100% in ITS) to be nested within subgenus *Euphorbia* (Figs. 10, 11). Both of these species are dwarf geophytes from India that are very different in appearance from the typical members of the subgenus. At least in the mature phase, they lack the characteristic spine-shield structure.

Euphorbia panchganiensis is apparently closely allied to *E. fusiformis* Hamilton ex D. Don, which was placed by Boissier in *E.* sect. *Rhizanthium* (= *E.* subg. *Rhizanthium* sensu Wheeler, 1943). Based on almost identical capsules and seeds, Gilbert (1987) first suggested that *E. fusiformis* might have evolved from Asian members of subgenus *Euphorbia*. The molecular evidence supports his suspicions. The reduction to geophytic herbs has been documented in at least one African lineage of subgenus *Euphorbia* (Carter, 1994), and it appears that the Indian geophytes represent a parallel derivation of this growth form from spiny shrubs. The Indian geophytic species should be examined at early ontogenetic stages to determine if indeed spine-shields are present in the seedlings.

Carter (1994) recognized two sections and many subsections in her classification of *Euphorbia* subg. *Euphorbia*, but not enough taxa were included in this study to test the validity of these groups.

Euphorbia *subg.* Lacanthis. *Lacanthis* Raf. (Rafinesque, 1837) originally contained only *Lacanthis splendens* Raf. (= *Euphorbia milii*). The name slipped into obscurity until Gilbert (1987) resurrected it at the rank of subgenus, applying it to a group of species from Madagascar previously treated together with the spine-shield taxa of *E.* subg. *Euphorbia*, sensu stricto, discussed above. Gilbert also included within subgenus *Lacanthis* (Raf.) Gilbert the species of *E.* sect. *Goniostema* Baill. ex Boiss. and the Madagascan members of *E.* subg. *Rhizanthium*. As discussed in detail (Gilbert, 1987), there are numerous differences that suggest these species should be treated separately from the narrowly defined subgenus *Euphorbia*. For example, in subgenus *Lacanthis* the inflorescences are much branched (vs. little branched), the bracts are well developed (vs. greatly reduced), and the seeds are oblong-cylindrical (vs. ovoid to subglobose). Additionally, in subgenus *Euphorbia* the spines are borne on a differentiated spine-shield and the stipules are represented by prickles just above the leaf, but in subgenus *Lacanthis* the spines are actually the stipules and a spine-shield is absent. Besides the Madagascan species, Gilbert also included in subgenus *Lacanthis* a few geophytes from tropical east Africa that are morphologically very similar to some of those from Madagascar.

A broad array of species from *Euphorbia* subg. *Lacanthis* were sampled. Those from Madagascar included *E. milii*, *E. pedilanthoides* Denis, *E. gottlebei* Rauh, *E. rossii* Rauh & Buchloh, *E. primulifolia*, *E. thouarsiana* Baill., *E. perrieri* Drake, *E. ankarensis* Boiteau, *E. millotii* Ursch & Leandri, *E. geroldii* Rauh, *E. capmanambatoensis* Rauh, and *E. iharanae* Rauh. From tropical East Africa, *E. rubella* Pax and *E. brunellii* Choiv. ex Chiarugi were represented. All taxa belong to clade C in a subclade containing subgenus *Euphorbia* and the *Synadenium* alliance (Figs. 10, 11). The tropical east African and the Madagascan taxa belong to different lineages within this subclade. The Madagascan members of subgenus *Lacanthis* are supported as a monophyletic assemblage belonging to a clade also containing species not previously associated with the group. *Euphorbia alluaudii* Drake, a Madagascan endemic very similar in habit to *E. tirucalli* but treated by Croizat (1972) in his *E.* sect. *Deuterocalli* Croizat, represents the earliest diverging species within the group. Another group not previously associated with subgenus *Lacanthis* is the *E. hedyotoides* complex of *E.* sect. *Denisophorbia*. In this analysis, the complex forms the sister clade to subgenus *Lacanthis* proper.

It is suggested that the origin of *Euphorbia* subg. *Lacanthis*, sensu Gilbert, is separate from that of subgenus *Euphorbia* and spinescence and succulence in these two groups have resulted from independent derivations.

Euphorbia *sect.* Arthrothamnus. Klotzsch and Garcke (1860) first proposed this group as a genus to accommodate *Euphorbia tirucalli* and seven species from the Cape Region of South Africa. Boissier (1862) later treated it as *Euphorbia* sect. *Arthrothamnus*. He removed *E. tirucalli* but expanded the group to include two species from the West Indies. The latter two were treated within his *E.* sect. *Arthrothamnus* subsect. *Americanae* Boiss., while the remainder of the Old World taxa were placed in section *Arthrothamnus* subsect. *Capenses* Boiss.

As discussed further under *Euphorbia* subg. *Agaloma*, the two subsections of *Arthrothamnus* do not appear closely related, and this section should be restricted to about 20 species in South Africa and Namibia. These are dioecious, dichotomously branching shrubs with photosynthetic, articulate branches and small, opposite leaves. Two species of the group were included here, *E. juttae* Dinter and *E. rhombifolia* Boiss., and the close relationship of both of these is well supported (bs 100% in both analyses, see Figs. 12, 14). They belong to clade D and represent an early diverging lineage of this clade. Further relationships of these species to other *Euphorbia* are unclear.

Euphorbia *subg.* Eremophyton. This group was first erected by Boissier (1862) as a section of *Euphorbia* to include *Euphorbia eremophila* A. Cunn., *E. agowensis* Hochst. ex Boiss., and *E. gueinzii*

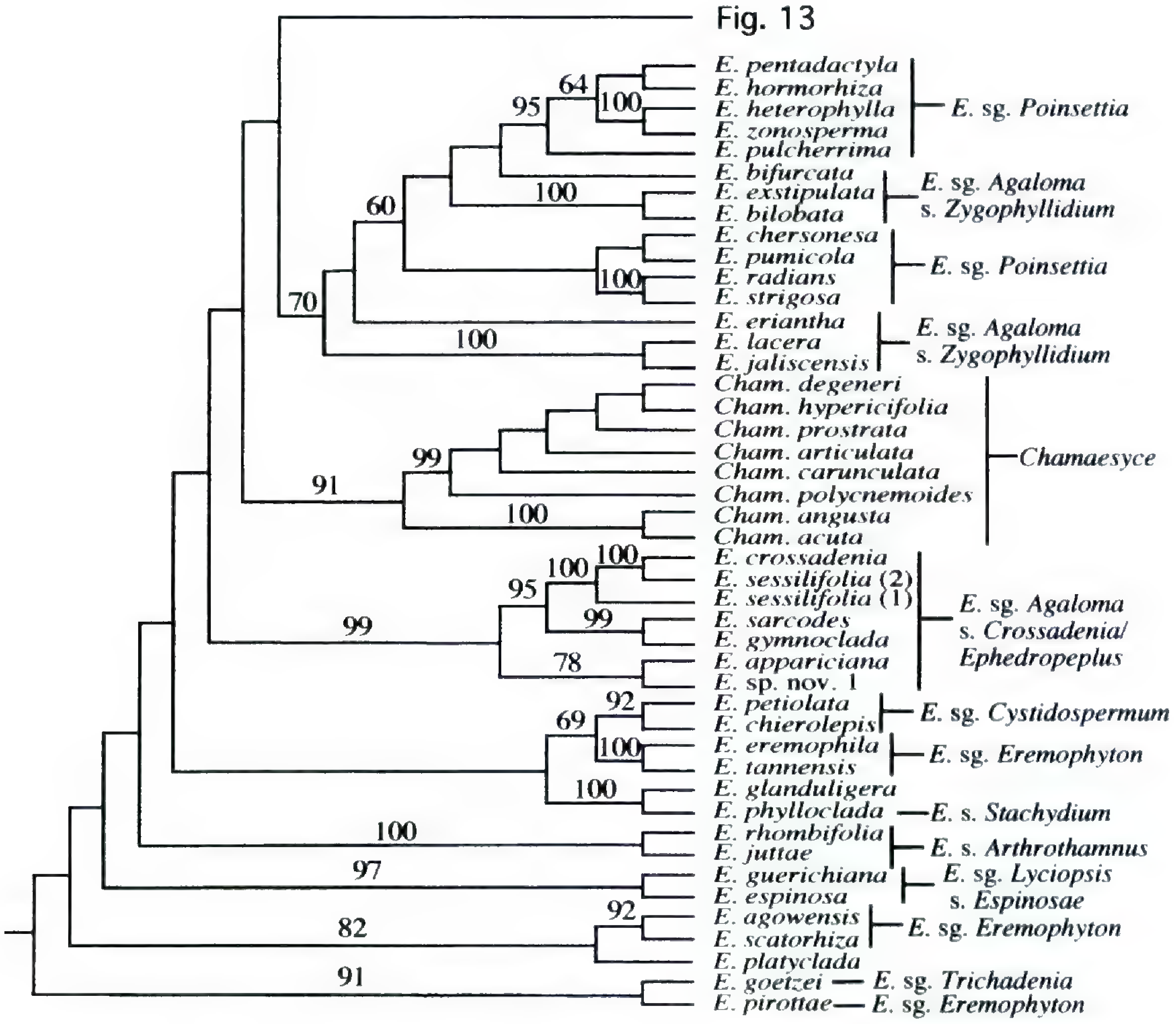

Figure 12. Euphorbiinae clade D (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *Cham.* = *Chamaesyce*, s. = section, sg. = subgenus.

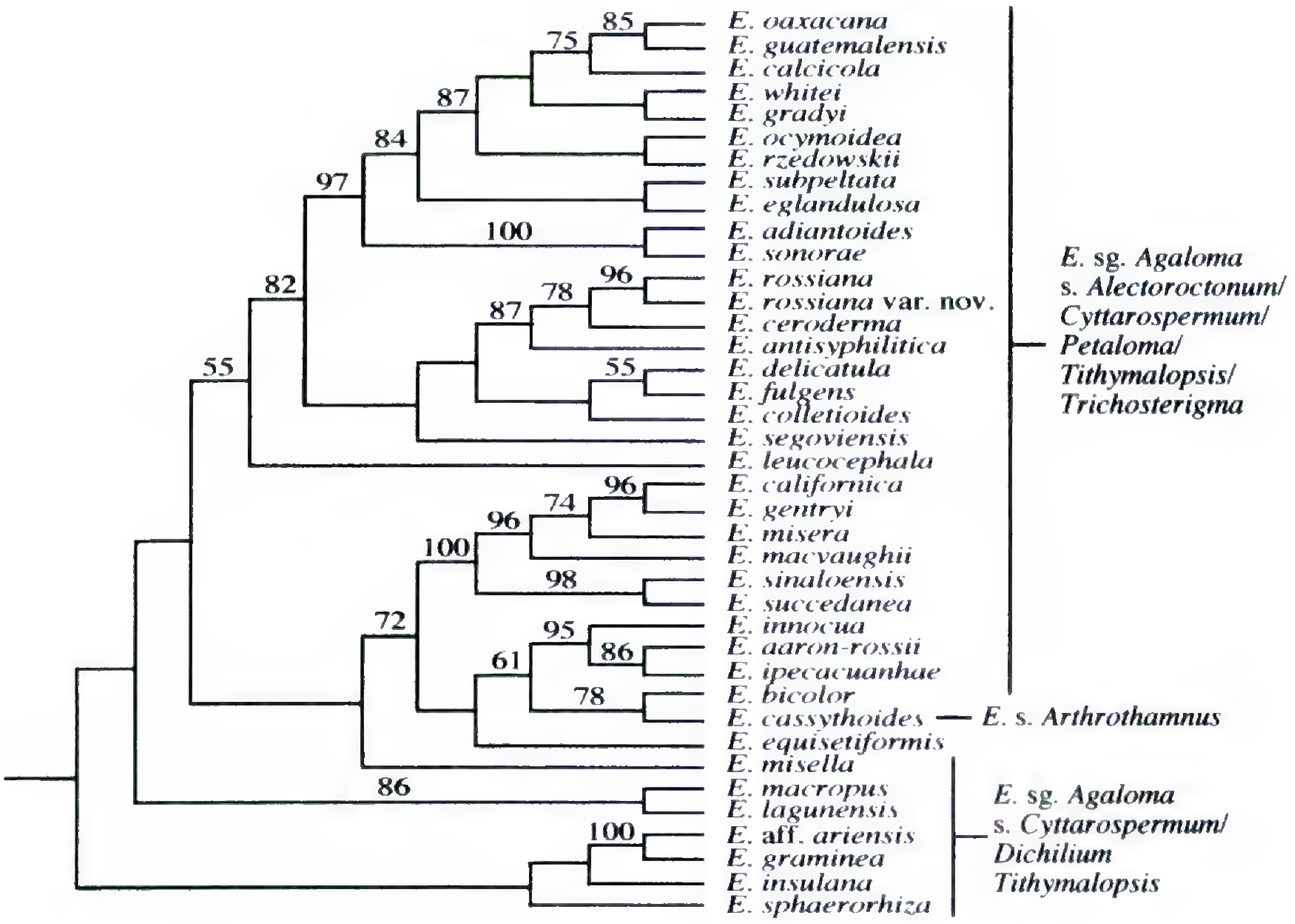

Figure 13. Euphorbiinae clade D (in part), strict consensus of 2160 trees based on a weighted maximum parsimony analysis of the ITS region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, s. = section, sg. = subgenus.

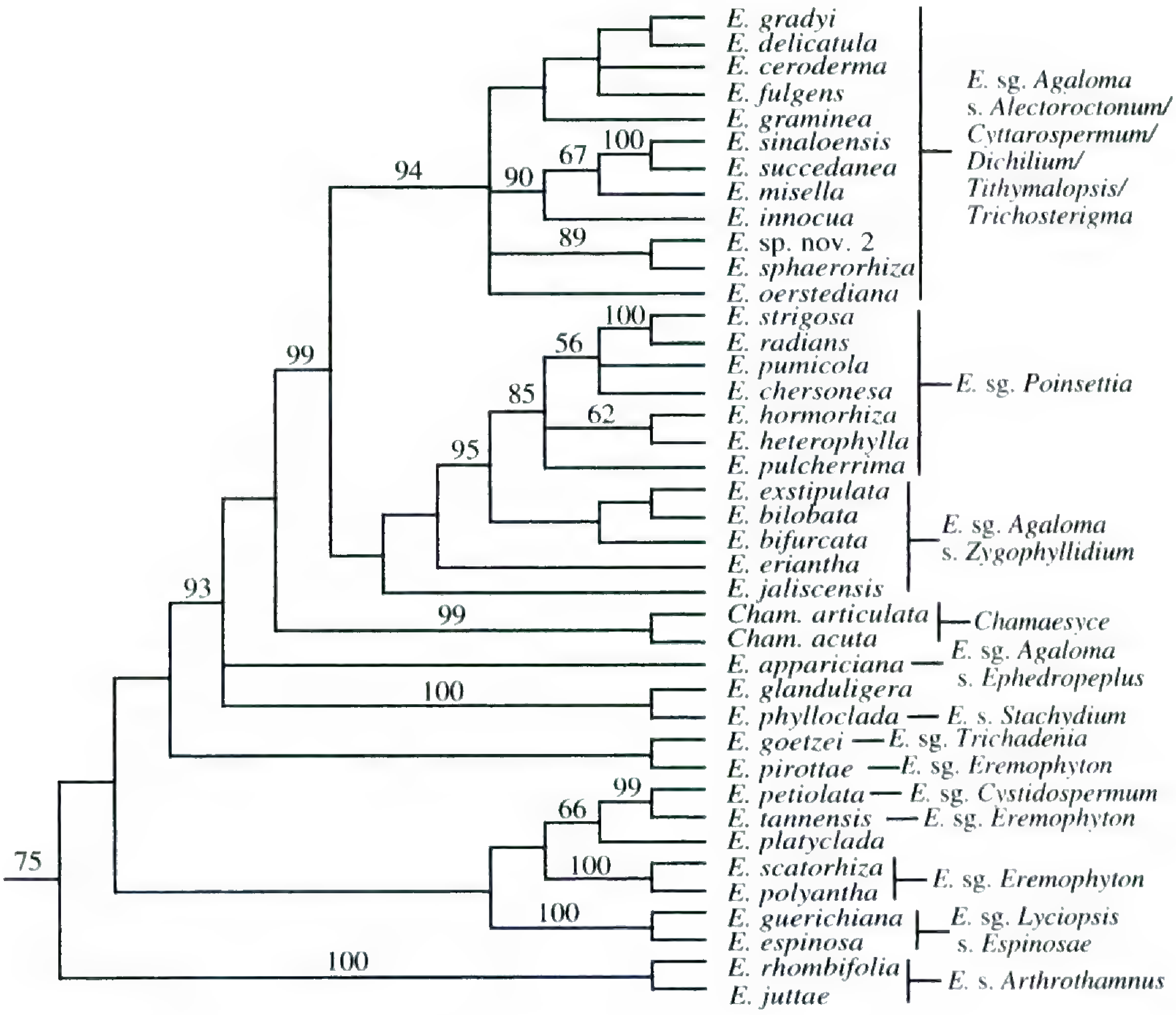

Figure 14. Euphorbiinae clade D, strict consensus of 19,012 trees based on a weighted maximum parsimony analysis of the *ndh*F region. Bootstrap values greater than 50% are shown above the branches. *E.* = *Euphorbia*, *Cham.* = *Chamaesyce*.

Boiss. It was originally circumscribed to contain herbs or subshrubs with alternate lower and opposite upper stem leaves; glandular or subulate stipules; axillary or terminal, solitary involucres with four to five glands lacking appendages; and carunculate to ecarunculate seeds. Carter (1985) emphasized also petiolate leaves and exserted capsules as characteristics of subgenus *Eremophyton*. As these traits suggest, there is no single synapomorphy that unites this group, and all of the features used to delineate the subgenus can be found in various combinations in other taxa of *Euphorbia*. In 1880, Bentham synonymized Boissier's *E.* sects. *Bongium* Boiss., *Cheirolepidium* Boiss., and *Pseudacalypha* under his expanded section *Eremophyton*, and this system was followed by Wheeler (1943) when he elevated the section to subgenus. *Euphorbia* sect. *Cheirolepidium* was removed by Prokhanov (1933) and formed the basis of his genus *Cystidopermum* Prokh. *Cystidospermum* was later reduced to a subgenus of *Euphorbia* (Prokhanov, 1949), and Radcliffe-Smith (1974) agreed that subgenus *Cystidospermum* was sufficiently distinct from the remainder of *E.* subg. *Eremophyton* to warrant its separate recognition. He additionally referred to it Boissier's *E.* sect. *Tithymalus* subsect. *Crotonopsideae*.

Two species of *Euphorbia* subg. *Cystidospermum* (sensu Radcliffe-Smith, 1974) were included in this study: *E. cheirolepis* and *E. petiolata* Banks & Sol. Various species of subgenus *Eremophyton* proper were also included: *E. boöphthona*, *E. pirottae*, *E. agowensis*, *E. scatorhiza* S. Carter, *E. cheirolepis*, *E. eremophila*, *E. tannensis* Spreng., *E. polyantha* Pax, *E. crotonoides*, *E. longituberculosa*, and *E. acalyphoides*. In the analyses these taxa do not group together and are widely scattered throughout the subtribe Euphorbiinae (Figs. 5, 6, 9, 11, 12, 14). Therefore, subgenus *Eremophyton*, as currently recognized, is highly polyphyletic.

The three species of *Euphorbia* subg. *Eremophyton* sect. *Pseudacalypha* included in this study (*E. acalyphoides*, *E. crotonoides*, and *E. longituberculosa*) all grouped as closely related members of clade A. However, they did not form a strictly monophyletic group but instead a grade of taxa (Figs. 5, 6). Interestingly, *E. matabelensis* (a member of subg. *Lyciopsis* sect. *Lyciopsis*) also occurred together with the species of subgenus *Eremophyton* sect. *Pseudacalypha* as sister to *Euphorbia croto-*

noides in the *ndh*F analysis, although there is no bootstrap support for this relationship and the two are morphologically very different.

One of the more unusual results of this study is the placement of *Euphorbia boöphthona*, an Australian member of subgenus *Eremophyton*, in a strongly supported clade (bs 94% in ITS) together with *E. plumerioides* and *E. haeleeleana*, two arborescent Pacific Island taxa presently treated in subgenus *Esula* sect. *Balsamis*. In most respects, *E. boöphthona* closely resembles other Australian members of subgenus *Eremophyton*, e.g., *E. tannensis* and *E. eremophila*, and these Australian taxa have been thought to represent a natural group (Hassall, 1977). It is worth noting that according to Hassall (1977), *E. boöphthona* differs from these two species as well as the other Australian members of the subgenus in being an octoploid (n = 28), but no tetraploid has yet been found in this subgenus.

Radcliffe-Smith's (1974) decision to unite Boissier's *Euphorbia* sect. *Tithymalus* subsect. *Crotonopsideae* (represented here by *E. petiolata*) with subgenus *Cystidospermum* (represented here by *E. cheirolepis*) was supported, and the two species are sister to each other (bs 92% in ITS, see Fig. 12) in this analysis. They belong to a clade also containing two members of *E.* subg. *Eremophyton* proper, *E. tannensis* and *E. eremophila*. Thus, subgenus *Cystidospermum* probably is best treated as a synonym of subgenus *Eremophyton*. The Madagascan endemic *E. platyclada* Rauh, whose relationship with other *Euphorbia* was previously unknown (Rauh, 1998), also groups with these taxa in the *ndh*F analysis, but this relationship is not well supported (Fig. 14). In the ITS analysis (Fig. 12), *E. platyclada* comes out with *E. scatorhiza* and *E. polyantha*. As suggested by Carter (1992b), these latter two species are sister taxa in so far as this sample is concerned.

Many species of *Euphorbia* subg. *Eremophyton* possess a great similarity to those of subgenus *Agaloma*, especially taxa of its section *Zygophyllidium* Boiss. For example, contrary to reports in the literature, the southwest Asian *E. petiolata* and *E. cheirolepis* actually possess involucral appendages. Undoubtedly, if these species occurred in the New World, they would be treated within subgenus *Agaloma* without question. Therefore, the molecular evidence that *E.* subg. *Agaloma* has either evolved from a portion of subgenus *Eremophyton* or that the two are sister taxa and share common ancestry is plausible.

Euphorbia *subg.* Agaloma. This taxon is based on another one of Rafinesque's genera, *Agaloma* Raf. It was first erected (Rafinesque, 1838) to accommodate *Euphorbia corollata* L. and two related species. Interestingly, Rafinesque also published six other genera that correspond to the current circumscription of this subgenus (*Aklema* Raf., *Lepadena* Raf., *Peccana* Raf., *Petaloma* Raf., *Vallaris* Raf., and *Zalitea* Raf.). *Euphorbia* subg. *Agaloma* was first treated at this rank by House (1924). At that time it only accommodated *E. corollata* L., and other members of modern subgenus *Agaloma* were placed in subgenus *Lepadena* (Raf.) House. Wheeler (1943) was the first to adopt subgenus *Agaloma* in its current circumscription, a concept corresponding to *E.* sect. *Adenopetalum* Boiss., sensu Bentham (1880) and Pax and Hoffmann (1931). The group is broadly defined to contain New World members of Euphorbiinae with petaloid involucral appendages but excludes species of *Chamaesyce* and *Pedilanthus*. Beside the presence of involucral appendages, little else unites all members of the group. Trees, shrubs, perennial herbs, geophytes, annuals, and stem-succulents are represented. The subgenus comprises about 150 species and is considered taxonomically difficult (Johnston, 1975; Buck & Huft, 1977). In addition, it has frequently been suspected of being paraphyletic, with both *Chamaesyce* and *E.* subg. *Poinsettia* nested within it.

Euphorbia subg. *Agaloma* was the best-sampled group in this study. Fifty-six species from all of its recognized sections were included. With the exception of two of these sections, *Euphorbia* sects. *Stachydium* and *Portulacastrum* (discussed previously), all species of subgenus *Agaloma* belong to clade D and form a single subclade (Figs. 12–14). Indeed, previous suspicions were supported, and both *Chamaesyce* and *E.* subg. *Poinsettia* are shown to have evolved from within subgenus *Agaloma*. Therefore, a monophyletic subgenus *Agaloma* must also include both *Chamaesyce* and *E.* subg. *Poinsettia*. This entire subclade is hereafter referred to as the *Agaloma* alliance.

The *ndh*F analysis strongly supports (bs 93%) that *Euphorbia phylloclada* and *E. glanduligera* Pax, two annual African species from the Namibian desert, also belong to the *Agaloma* alliance (Fig. 14). Both species possess well-developed involucral appendages and morphologically are easily accommodated within subgenus *Agaloma*, where they certainly would have been placed if it were not for their African distribution. Boissier treated *Euphorbia phylloclada* as the sole representative of *E.* sect. *Stachydium* subsect. *Capensis*. However, the molecular data do not support a close relationship be-

tween this species and other members of the section (see discussion under *E.* sect. *Stachydium*). Pax (1894b) placed *E. glanduligera* in *Chamaesyce*, and the similarity is indeed strong. In the ITS analysis, these two species are placed in a clade sister to some members of subgenus *Eremophyton* (Fig. 12). However, this relationship lacks any bootstrap support, and the *ndh*F analysis probably provides a more accurate reflection of relationships.

Within the New World, the earliest diverging group in the *Agaloma* alliance consists of *Euphorbia* subg. *Agaloma* sects. *Ephedropeplus* Müll. Arg. and *Crossadenia* Boiss. The former section is represented here by *E. appariciana* Rizzini, *E.* sp. nov. 1, and *E. gymnoclada* Boiss., while the latter section is represented here by *E. crossadenia*, *E. sessilifolia*, and *E. sarcodes*. In the ITS analysis, these two sections form a single well-supported clade (bs 99%) sister to the remainder of the *Agaloma* alliance (Figs. 12, 13). The sample in the *ndh*F study was not sufficient to investigate their monophyly, but here too the single species included, *E. appariciana*, is sister to the remainder of the *Agaloma* alliance. Both sections are restricted to eastern Brazil and represent a morphologically diverse assemblage of about a dozen arid-adapted perennial herbs, small shrubs, or stem succulents. The involucral appendages are deeply cleft to subentire, and in one species they are lacking. Traditionally subgenus *Agaloma* sects. *Crossadenia* and *Ephedropeplus* have been separated by the possession of opposite or whorled, highly reduced scalelike leaves in section *Ephedropeplus* and the possession of alternate, well-developed leaves in section *Crossadenia*. However, this distinction does not appear to hold, and with respect to each other, the sections are not monophyletic. Therefore, *E.* subg. *Agaloma* sect. *Ephedropeplus* is best reduced to synonymy under section *Crossadenia*.

In both the ITS and *ndh*F analyses, *Chamaesyce* is the next diverging lineage in the *Agaloma* alliance, and it is sister to the remainder of the species, excluding the earlier diverging Namibian taxa and members of *Euphorbia* subg. *Agaloma* sect. *Crossadenia* (Figs. 12–14). However, statistical support for this topology is lacking. What is supported is that *Chamaesyce* is an ancient lineage that diverged earlier in the evolution of the *Agaloma* alliance. Beyond this, however, the exact relationship of its members to other Euphorbiinae is not evident.

After the divergence of *Chamaesyce*, there are two major groups within the *Agaloma* alliance. These are sister to each other and present in both the ITS and *ndh*F analyses, with considerable support (bs 99%) in the latter (Figs. 12–14). The first clade contains species currently placed in *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* together with members of subgenus *Poinsettia*; the second clade contains the remainder of sections treated in subgenus *Agaloma*.

Euphorbia subg. *Agaloma* sect. *Zygophyllidium* corresponds to a North American and Mexican assemblage of about a dozen species. The group is poorly defined, but united by their annual or rarely short-lived perennial habit. In addition, many species possess serrate leaves. The section was represented in this study by *E. bifurcata* Engelm., *E. bilobata* Engelm., *E. eriantha* Benth., *E. exstipulata* Engelm., *E. jaliscensis* B. L. Rob. & Greenm., and *E. lacera* Boiss. It is not monophyletic because subgenus *Poinsettia* is nested within it (see discussion under *E.* subg. *Poinsettia*).

Sister to the *Zygophyllidium*/*Poinsettia* group is the core of *Euphorbia* subg. *Agaloma*, an assemblage comprised of section *Alectoroctonum* (Schltdl.) Baill. (representatives: *E. colletioides* Benth., *E. leucocephala* Lotsy, and *E.* sp. nov. 2), section *Cyttarospermum* Boiss. (representatives: *E. adiantoides* Lam., *E.* aff. *ariensis* HBK, *E. calcicola* Fern., *E. delicatula* Boiss., *E. eglandulosa* V. W. Steinm., *E. gradyi* V. W. Steinm. & A. Ram.-Roa, *E. graminea* Jacq., *E. guatemalensis* Standl. & Steyerm., *E. lagunensis* Huft, *E. misella* S. Watson, *E. oaxacana* B. L. Rob. & Greenm., *E. ocymoidea* L., *E. rzedowskii* McVaugh, *E. segoviensis* (Klotzsch & Garcke) Boiss., *E. sinaloensis* Brandegee, *E. sonorae* Rose, *E. subpeltata* S. Watson, *E. succedanea* L. C. Wheeler, and *E. whitei* L. C. Wheeler), section *Dichilium* Boiss. (representatives: *E. insulana* Vell. and *E. oerstediana* (Klotzsch & Garcke) Boiss.), section *Petaloma* (Raf.) Boiss. (representative: *E. bicolor* Engelm. & A. Gray), section *Tithymalopsis* (Klotzsch & Garcke) Boiss. (representatives: *E. aaron-rossii* A. H. Holmgren & N. H. Holmgren, *E. innocua* L. C. Wheeler, *E. ipecacuanhae* L., *E. macropus* (Klotzsch & Garcke) Boiss., and *E. sphaerorhiza* Benth.), and section *Trichosterigma* (Klotzsch & Garcke) Boiss. (representatives: *E. antisyphilitica* Zucc., *E. californica* Benth., *E. ceroderma* I. M. Johnst., *E. fulgens* Karw. ex Klotzsch, *E. gentryi* V. W. Steinm. & T. F. Daniel, *E. macvaughii* Carvajal & Lomelí, *E. misera* Benth., *E. rossiana* Pax, and *E. rossiana* var. nov.). In comparison to members of subgenus *Agaloma* sect. *Zygophyllidium*, species of this group are highly variable in habit, and the leaves are strictly entire. This group accounts for nearly 90% of the species that have been treated in subgenus *Agaloma*, and it ranges from Argentina and Chile to

the northern United States and the Caribbean. Collectively, these sections form a monophyletic group in both analyses. However, the clade only has bootstrap support (94%) in the *ndh*F analysis (Fig. 14). Here too belong *E. cassythoides* Boiss., a Caribbean taxon previously placed in *Euphorbia* sect. *Arthrothamnus* (Boissier, 1862) and *E. equisetiformis* A. Stewart, an endemic to the Galapagos Islands whose relationship to other *Euphorbia* was uncertain (Burch, 1971).

Although the sample of species is not broad enough to make a definitive conclusion, this study supports Park's (1998) narrow circumscription of *Euphorbia* subg. *Agaloma* sect. *Tithymalopsis*. According to the molecular data, the section, as defined by Huft (1979) and Boissier (1862), is polyphyletic and composed of at least three separate lineages. However, neither Huft nor Boissier can be criticized. In fact, the placement of similar-appearing, geophytic taxa such as *E. macropus* and *E. sphaerorhiza* in separate clades with nongeophytic taxa is odd and represents one instance where molecular results are counterintuitive. Of the remaining five sections of subgenus *Agaloma*, only sections *Petaloma* and *Dichilium* are likely to be monophyletic, but not enough taxa from these were included to test this hypothesis. What is clearly shown is that subgenus *Agaloma* sects. *Alectoroctonum*, *Cyttarospermum*, and *Trichosterigma* are polyphyletic.

Euphorbia *subg.* Poinsettia. According to the most recent treatment of *Euphorbia* subg. *Poinsettia* (Mayfield, 1997), this taxon is a strictly New World assemblage of 24 species. Dressler (1962) recognized 11 species. The group is characterized by cup-shaped involucral glands that are generally reduced to one (rarely more) per involucre. Pigmentation of the subcyathial leaves, as exemplified by *E. pulcherrima*, occurs in many but not all of the species. Growth form varies from annuals, perennial herbs, geophytes, to shrubs. Nine species of subgenus *Poinsettia* were included in this study: *E. chersonesa* Huft, *E. heterophylla* L., *E. hormorhiza* Radcl.-Sm., *E. pentadactyla* Griseb., *E. pulcherrima*, *E. pumicola* Huft, *E. radians* Benth., *E. strigosa* Hook. & Arn., and *E. zonosperma* Müll. Arg.

In both analyses, these species are nested within a clade that corresponds to *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* (Figs. 12, 14). This is not surprising because some species of this section (e.g., *E. bifurcata*) possess involucres with a single gland and nearly identical seeds to those of members of subgenus *Poinsettia*. In addition, other taxa (e.g., *E. jaliscensis*) possess panduriform leaves that are otherwise known only from a few species of subgenus *Poinsettia*. The subgenus is noteworthy because of the extreme amount of genetic divergence among its members. It forms a monophyletic group only in the *ndh*F analysis (Fig. 14). In the ITS analysis, subgenus *Poinsettia* comes out in two groups nested within subgenus *Agaloma* sect. *Zygophyllidium* (Fig. 12). A close affinity between subgenus *Poinsettia* and species of subgenus *Agaloma* sect. *Dichilium* has been suggested (Dressler, 1962; Webster, 1967), but the two groups do not appear closely related (Figs. 12–14). Dressler's (1962) removal of *E. eriantha* from subgenus *Poinsettia* is justified by molecular evidence. *Euphorbia chersonesa* (= *E. heterophylla* L. var. *eriocarpa* Millsp.) was placed in subgenus *Poinsettia* by Millspaugh (1889) but placed in subgenus *Agaloma* by Huft (1984). The molecular data strongly support that it is sister to *E. pumicola* in subgenus *Poinsettia*. Morphologically, *E. chersonesa* is noteworthy because it is intermediate between subgenus *Agaloma* sect. *Zygophyllidium* and other members of subgenus *Poinsettia* in involucral gland characteristics; the glands are not deeply cupped, but they do apparently lack appendages.

The herbaceous habit of the species of *Euphorbia* subg. *Agaloma* sect. *Zygophyllidium* and many of the early diverging members of subgenus *Poinsettia* suggests that woodiness in species such as *E. pulcherrima* is secondarily derived. In addition, the lack of involucral appendages appears to represent a reversal to unappendaged involucres.

ORIGIN AND BIOGEOGRAPHY OF EUPHORBIEAE

The tribe Euphorbieae demonstrates a complex biogeographical pattern. The earliest diverging clade, subtribe Anthosteminae, is strictly African and Madagascan (Figs. 1, 2). The next diverging clade, subtribe Neoguillauminiinae, occurs in Australia and New Caledonia (Figs. 1, 2). Of the four major clades of Euphorbiinae, one, clade A (Figs. 5, 6), is strictly African and Madagascan, and one, clade B (Figs. 7, 8), is primarily distributed in temperate regions of the Northern Hemisphere. The two remaining clades, C (Figs. 9–11) and D (Figs. 12–14), are widespread, but the earliest diverging lineages within these two clades occur in Africa and Madagascar. If present-day distributions are indicative of historical ranges, then the molecular evidence is consistent with a hypothesized African origin of the tribe before the breakup of Gondwanaland.

Although clade B is almost entirely Laurasian in distribution, there are a few members in Africa. The

clade is absent from Australia and essentially absent from South America, where only two species occur, *Euphorbia spathulata* and *E. philippiana* Boiss. The first of these has an amphitropical distribution and also occurs in North America. The second is a Chilean endemic similar to North American species. Considering that approximately 85% of the temperate South American species of angiosperms have an origin in the Northern Hemisphere (Raven, 1963), the presence of these species in South America is likely the result of dispersal events from North America. Within clade B there are two major subclades, and both possess species in North America and Eurasia. It is possible that the current distribution of clade B represents either an ancient dispersal event to Laurasia or evidence that the diversification of Euphorbiinae predates the split up of Pangaea.

Clade C has a wide distribution that is best described as pantropical. According to the *ndh*F results herein, the earliest diverging lineages of this clade occur in Africa, Madagascar, and Australasia. The Hawaiian endemic species *Euphorbia haeleeleana* belongs here and appears to have arrived at the islands by long-distance dispersal from related taxa, e.g., *Euphorbia plumerioides*, in the Pacific Islands. In the *ndh*F analysis, all of the Neotropical members of clade C form a single lineage that is sister to a lineage containing the subgenera *Euphorbia* and *Lacanthis* together with the *Synadenium* alliance, again suggesting that these two groups arose before the breakup of Gondwanaland. Similarly, the sister clade relationship of subgenus *Lacanthis* and subgenus *Euphorbia* together with the *Synadenium* alliance suggest that the common ancestor of both these groups was present before Madagascar began to separate from Africa.

Clade D has a distribution similar to clade C. Both ITS and *ndh*F analyses indicate that the earliest diverging lineages are in Africa, Madagascar, and southwest Asia. Also like in clade C, all of the New World species belong to a single lineage. Interestingly, according to the *ndh*F evidence, of the two earliest-diverging groups in the lineage containing the New World taxa of clade D, one occurs in Namibia and the other occurs in arid eastern Brazil. Thus, there is a clear, well-supported link between New and Old World species in this group.

The near parallel distribution in the sister clades C and D provides further evidence that the distribution of New and Old World taxa is the result of vicariance caused by the breakup of Gondwanaland. Therefore, the molecular evidence corroborates that despite being a very specialized group, the Euphorbiinae are also a very ancient group. Based on biogeographic patterns, Croizat (1940) postulated that *Euphorbia* was already differentiated into modern subgenera by the mid Cretaceous (ca. 100 million years ago), and this appears quite possible.

The fruits in Euphorbieae are generally dry, explosively dehiscent, and initially dispersed only a few meters from their source. For this reason, there are few instances of long-distance dispersal within the tribe. One notable exception involves species of *Chamaesyce*, a primarily New World taxon whose range parallels that of the entire Euphorbieae. Webster (1967) proposed that this group probably originated in the New World and molecular evidence supports his hypothesis. Because many *Chamaesyce* possess mucilaginous seeds, much of their great success in distribution is likely because seeds are able to adhere to animals and thus achieve long-distance dispersal (see discussion in Jordan & Hayden, 1992). This feature is otherwise rare in *Euphorbia* and helps explain why *Chamaesyce* is one of the few relatively derived taxa within Euphorbiinae that exhibits a transoceanic distribution.

Webster et al. (1982) stated that the most-likely primitive Euphorbiinae were in *Euphorbia* sect. *Denisophorbia*. Dressler (1957) believed that they were in sections *Balsamis* and *Adenorima*. Although the molecular evidence does not support their hypotheses, it does not provide solid insight as to what actually is the most primitive *Euphorbia* either, and it appears difficult to identify a single most-ancestral group. Dressler's and Webster's choices are sound because all three sections represent early diverging lineages within the genus.

The molecular evidence does provide some insight as to the features that ancestral *Euphorbia* likely possessed. First, they were probably a tropical tree or shrub, because early diverging lineages within the various clades of *Euphorbia* are mostly woody tropical plants. Phyllotaxy was presumably spiral, and it is likely that a pseudoumbellate inflorescence structure was well developed; these characteristics are found in all the major clades of *Euphorbia*, and their widespread presence is parsimoniously explained by their presence in the common ancestor of all four major clades. Stipules were probably absent or minute and glanduliform. There were likely five glands on the involucre. Although gland reduction is common, in many species with reduced glands, e.g., *E. graminea* Jacq., the first involucre formed in an inflorescence often possesses five glands and only subsequent involucres possess fewer glands. Presumably involucral appendages were absent, because they are present only in derived groups of Euphorbiinae. It is note-

worthy that the Madagascan endemic *Euphorbia antso* is the least derived species with regard to molecular evolution (see Figs. 3, 4) and possesses most of the features discussed above as ancestral. Although the ancestral condition is probably woody, in terms of species number, the two most successful lineages within the subtribe, *Chamaesyce* and the temperate *E.* subg. *Esula* clade, are primarily comprised of herbaceous species.

The large amount of diversification within Euphorbiinae compared to the other subtribes of Euphorbieae and the sister tribe Hippomaneae suggests that one or more key innovations may have promoted rapid evolution and diversification within this lineage. If such innovations actually exist, they likely involve the cyathium. Although cyathiate inflorescences also occur in Anthosteminae and Neoguillauminiinae, both these subtribes contain very few species and have narrow distributions. The particular feature that occurs in Euphorbiinae but is absent in the other subtribes is that, with few exceptions, the nectar-producing involucral glands are situated on the rim of the involucre and not partially enclosed within this structure. Therefore, this feature may have greatly enhanced successful insect attraction and pollination, thus giving members of Euphorbiinae a selective advantage, which in turn has driven the patterns of speciation and diversification presently observed in extant members of the subtribe.

COMPARISON WITH MORPHOLOGICAL DATA

There are two previous phylogenetic studies of the Euphorbieae based on morphological characters (Park, 1996; Park & Elisens, 2000). The first of these treated only the New World taxa of subtribe Euphorbiinae, while the second treated the entire tribe. The molecular results differ drastically from the results obtained in either analysis. Even the two separate morphological analyses yielded different topologies, and in neither study was there significant statistical support for the majority of the clades. Part of the problem with these morphological analyses may be that too few characters were included to resolve the taxa. For example, in the first study of the New World species only 37 characters were used to resolve relationships among 49 terminal taxa, in this case species groups. In addition, many characters employed in both analyses are highly variable even among closely related species, and their use to discern relationships within such a large and diverse tribe as Euphorbieae is unlikely to provide accurate results.

FUTURE OF EUPHORBIINAE CLASSIFICATION

The current classification of Euphorbieae subtribes Anthosteminae and Neoguillauminiinae is well supported herein and recognizes only monophyletic groups. No taxonomic adjustments are necessary for these subtribes, but as mentioned above, problems remain for the classification of subtribe Euphorbiinae.

The current taxonomic trend is going in the direction of splitting *Euphorbia.* This has already been observed with Webster's (1967) removal of *Chamaesyce.* More recently, Carter (1994: 378) stated that subgenus *Euphorbia* "could be separated as a genus in its own right." Likewise, Gilbert (1987: 235) also leaned toward an eventual dismemberment of *Euphorbia,* but well aware of the "profound nomenclatural consequences" associated with such a change, he justified only changes in rank within *Euphorbia.*

We disagree that *Euphorbia* should be divided. Our opinion is that the best long-term solution to the problem of Euphorbiinae classification is to expand *Euphorbia* to encompass all members of the subtribe. Some might contend that this is an undesirable step backward 250 years to Linnaeus's broad concept of *Euphorbia.* However, we believe that this solution is more favorable than leaving the genus in its current paraphyletic circumscription or restricting *Euphorbia* to only the subgenus *Euphorbia.*

The first taxonomic problem with limiting *Euphorbia* to subgenus *Euphorbia* is that ca. 90% of the species currently in the genus would need to be accommodated in other genera. Thus, *Euphorbia,* a well-known and easily identifiable taxon known throughout the world, would no longer exist in most parts of the globe. Instead, there would be a multitude of genera completely unknown to most, and the boundaries and circumscription of these would be vague and certainly debated for quite some time. On the contrary, a broad *Euphorbia* would require changing the names of ca. 100 (vs. ca. 1700!) species and would only affect groups with relatively limited distributions. These changes would only mildly broaden the current concept of *Euphorbia* to encompass taxa that possess an unusual involucral morphology, a feature we believe has received undue taxonomic weight.

Another reason that splitting *Euphorbia* is unsatisfactory concerns the unusual nature of evolution within this group. The situation here is that basic cyathial morphology in the genus is highly conserved, but vegetative morphology is highly plastic. This has led to much parallel evolution in

growth form with little change in floral form. Therefore, if the relationships suggested by the molecular evidence do indeed accurately depict the phylogeny of the group, then there are a number of well-defined monophyletic lineages nested within a paraphyletic background of relatively undifferentiated groups or groups that have undergone a high degree of parallel vegetative evolution.

To propose various genera whose members are superficially nearly identical fails to serve one of the primary purposes of a system of classification, i.e., to provide a predictable system that allows for the separation of taxa and for the ability to make assumptions about relationship based on morphological features. If *Euphorbia* classification is to actually reflect relationship, then there will be exceptions and inconsistencies in defining new genera. We fear that any system that attempts to dismember *Euphorbia* will continue to have only limited success and acceptance.

Croizat (1965: 574) emphasized the problem associated with subgeneric groups within *Euphorbia* and stated "the infraspecific combinations of characters are so intricate as to make it really difficult to identify a truly natural subgeneric taxon." The same problem occurs with an elevation in rank to genus, but the broad implications are greatly more severe. Recognizing highly similar subgeneric taxa is much less of a problem because such rank is usually of primary interest to specialists in the group. Webster (1967: 398) stated, "If the various microgenera of Euphorbieae cannot be easily distinguished, there seems little reason to adopt them simply because they represent evolutionary units; it is quite easy to discuss the evolution of these taxa if they are referred to as infrageneric components of *Euphorbia*." We could not agree more.

As mentioned in the introduction, the majority of genera currently segregated from *Euphorbia* are distinguished by cyathial traits. In some regards, cyathial morphology has received undue weight, and this may be because there has been great diversification in vegetative morphology throughout Euphorbiinae, but the overall structure of the cyathium has remained relatively conserved. Thus, changes in cyathial morphology are viewed as taxonomically significant occurrences, and little systematic emphasis has been placed on other features, including relationships. Leach (1973: 32), when describing *Endadenium*, justified his new genus on the basis of its distinctive arrangement of glands within the involucre, further saying that *Endadenium* "combines so many of the characteristics of the other African members of the tribe that its assignment to any one of the genera involved would so effectively blur, if not nullify, the diagnostic criteria as to make it virtually impossible to retain these as separate genera on any but purely arbitrary grounds." However, the current recognition of genera separated solely on the basis of cyathial characters while ignoring, as in the case of *Endadenium*, all of the characters that do indeed blend the segregate genera into *Euphorbia*, is in itself somewhat arbitrary.

One of the arguments frequently used to justify the division of *Euphorbia* is that the genus is so large and heterogeneous that it is unwieldy. The incredible speciation and diversification that have occurred within *Euphorbia* are largely biological facts. Dismembering the genus would make it smaller and less heterogeneous but collectively as unwieldy an assemblage as ever. Another argument advocated by splitters is that the generic concept used for these assemblages is too broad in comparison with other groups; for the sake of taxonomic consistency, *Euphorbia* must be divided. In response to this, it is worth pointing out that no two lineages of plants are completely comparable to each other. Each has an independent evolutionary history. Therefore, the argument that *Euphorbia* should be divided simply because its evolutionary past has involved amazing speciation, dispersal, and diversification is unfounded. In our opinion, recognizing the genus in its broad sense has some benefit because it conveys the incredible evolutionary history of this group.

Can a workable system of classification be developed for the Euphorbiinae that is based on the concept of monophyly? We believe that the answer is yes, but the units of such a classification should be infrageneric. Certainly many modifications will be necessary and time required before a stable system of classification is developed. However, it is better that such a process be undertaken at the infrageneric level, where the far-reaching nomenclatural implications associated with generic changes can be avoided.

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Appendix 1. Voucher information for the included species of Euphorbieae and outgroups sequenced in this study. For cultivated and introduced taxa, the native origin of the plant is given in parentheses.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
OUTGROUPS			
Omalanthus populifolius Graham	Cultivated (nat. Australia), *Steinmann 1423* (RSA)	AF537585	AF538262
Sapium sebiferum (L.) Roxb.	Cultivated (nat. China), *Steinmann 1424* (RSA)	AF537586	AF538261
Sebastiania cornuta McVaugh	Mexico, Sonora, *Steinmann 589* (RSA)	AF537587	AF538263
Stillingia spinulosa Torr.	Mexico, Sonora, *Felger 92-381* (RSA)	AF537588	AF538264
EUPHORBIEAE SUBTRIBE ANTHOSTEMINAE			
Anthostema madagascariense Baill.	Madagascar, *Pascal 586* (MO)	AF537582	AF538257
Anthostema senegalense A. Juss.	Senegal, *Bamps 7759* (MO)	—	AF538259
Anthostema sp. nov.	Madagascar, *Miller et al. 8840* (MO)	AF537583	AF538258
Dichostemma glaucescens L. Pierre	Gabon, *McPherson 15531* (DAV)	AF537584	AF538260
EUPHORBIEAE SUBTRIBE NEOGUILLAUMINIINAE			
Calycopeplus casuarinoides L.S. Sm.	Cultivated (nat. Australia), *Steinmann 1407* (RSA)	AF537580	—
Calycopeplus collinus P.I. Foster	Australia, *van der Werff 11848* (DAV)	—	AF538254
Calycopeplus paucifolius (Klotzsch) Baill.	Australia, *Craven 7139* (RSA)	—	AF538255
Neoguillauminia cleopatra (Baill.) Croizat	New Caledonia, *McPherson 17882* (MO)	AF537581	AF538256
EUPHORBIEAE SUBTRIBE EUPHORBIINAE			
Chamaesyce acuta (Engelm.) Millsp.	U.S.A., Texas, *Mayfield 1989* (RSA)	AF537450	AF538176
Chamaesyce angusta (Engelm.) Small	Mexico, Coahuila, *Mayfield 1328* (RSA)	AF537449	—
Chamaesyce articulata (Burm.) Britton	U.S.A., Virgin Isalnds, *Steinmann 94-10* (RSA)	AF537446	AF538175
Chamaesyce caruneulata (Waterf.) Shinners	Mexico, Chihuahua, *Bowers et al. 2939* (ARIZ)	AF537447	—
Chamaesyce degeneri (Sherff) Croizat & Degener	U.S.A., Hawaii, *Motley 338* (NY)	AF537444	—
Chamaesyce hypericifolia (L.) Millsp.	U.S.A., Hawaii, *Motley 1804* (NY)	AF537443	—
Chamaesyce prostrata (Aiton) Small	U.S.A., Hawaii, *Motley 1802* (NY)	AF537445	—
Chamaesyce polycnemoides (Boiss.) J. Soják	Botswana, *Snow & Chatakuta 6905* (MO)	AF537448	—
Endadenium gossweileri (N.E. Br.) L.C. Leach	Cultivated (nat. Angola), *Steinmann 1457* (RSA)	AF537471	AF538198
Euphorbia aaron-rossii A.H. Holmgren & N.H. Holmgren	U.S.A., Arizona, *Ross s.n.* (RSA)	AF537396	—
Euphorbia abdelkuri Balf.f.	Cultivated (nat. Abd-el-Kuri), *Steinmann 1437* (RSA)	AF537458	AF538194
Euphorbia acalyphoides Hochst. ex Boiss.	Kenya, *Luke et al. TPR177* (MO)	AF537576	AF538251
Euphorbia acanthothamnus Heldr. & Sart. ex Boiss.	Cultivated (nat. Greece/Turkey), *Steinmann 1425* (RSA)	AF537554	AF538232
Euphorbia adiantoides Lam.	Ecuador, *Harling & Anderson 22548* (GB)	AF537395	—
Euphorbia agowensis Hochst. ex Boiss.	Ethiopia, *Gilbert & Thulin 132* (MO)	AF537419	—
Euphorbia alluaudii Drake	Cultivated (nat. Madagascar), *Steinmann 1481* (RSA)	AF537468	AF538197
Euphorbia alta Norton	U.S.A., Arizona, *Sanders 5905* (RSA)	AF537553	—
Euphorbia amygdaloides L.	Cultivated (nat. Europe), *Steinmann 1428* (RSA)	AF537544	—

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia ankarensis Boiteau	Cultivated (nat. Madagascar), *Steinmann 1482* (RSA)	AF537462	—
Euphorbia antisyphilitica Zucc.	Cultivated (nat. U.S.A., Texas), *Steinmann 1451* (RSA)	AF537398	—
Euphorbia antso Denis	Cultivated (nat. Madagascar), *Steinmann 1473-B* (RSA)	AF537579	AF538253
Euphorbia aphylla Brouss. ex Willd.	Cultivated (nat. Canary Islands), *Steinmann 1466* (RSA)	AF537540	AF538225
Euphorbia appariciana Rizzini	Cultivated (nat. Brazil), *Steinmann 1442* (RSA)	AF537455	AF538177
Euphorbia arbuscula Balf.f.	Cultivated (nat. Socotra), *Steinmann 1435* (RSA)	AF537496	—
Euphorbia aff. *ariensis* HBK	Mexico, Nayarit, *Steinmann 1148* (RSA)	AF537409	—
Euphorbia atrispina N.E. Br.	Cultivated (nat. Republic of S. Africa), *Steinmann 1478* (RSA)	AF537568	—
Euphorbia atropurpurea Brouss. ex Willd.	Cultivated (nat. Canary Islands), *Steinmann 1489* (RSA)	AF537542	AF538230
Euphorbia attastoma Rizzini	Cultivated (nat. Brazil), *Steinmann 1487* (RSA)	AF537511	—
Euphorbia balsamifera Aiton ssp. *adenensis* (Deflers) Bally	Cultivated (northeast tropical Africa), *Steinmann 1480* (RSA)	AF537571	AF538250
Euphorbia bicolor Engelm. & A. Gray	U.S.A., Texas, *Van Devender 96-290* (RSA)	AF537386	—
Euphorbia bifurcata Engelm.	Mexico, Nuevo León, *Nesom 7703* (RSA)	AF537434	AF538173
Euphorbia bilobata Engelm.	U.S.A., Arizona, *Steinmann 938* (RSA)	AF537435	AF538172
Euphorbia boöphthona C.A. Gardner	Australia, *Coveny 3054* (RSA)	AF537515	AF538207
Euphorbia brunellii Chiov.	Cultivated (nat. east tropical Africa), *Steinmann 1495* (RSA)	AF537486	AF538203
Euphorbia calcicola Fern.	Mexico, Morelos, *Steinmann 801* (RSA)	AF537385	—
Euphorbia californica Benth.	Cultivated (nat. Mexico), *Steinmann 1492* (RSA)	AF537377	—
Euphorbia calyculata HBK	Mexico, Puebla, *Tenorio L. 7261c* (NY)	AF537524	AF538221
Euphorbia calyptrata Coss. & Kralik	Morocco, *Podlech 45138* (RSA)	AF537549	—
Euphorbia capmanambatoensis Rauh	Cultivated (nat. Madagascar), *Steinmann 1468* (RSA)	AF537476	—
Euphorbia caputmedusae L.	Cultivated (nat. Republic of S. Africa), *Steinmann 1463* (RSA)	AF537574	—
Euphorbia cassythoides Boiss.	Cayman Islands, *Proctor 47858* (NY)	AF537387	—
Euphorbia ceroderma I.M. Johnst.	Mexico, Sonora, *Steinmann 1393* (RSA)	AF537389	AF538153
Euphorbia cestrifolia HBK	Ecuador, *Harling 27200* (GB)	AF537521	AF538213
Euphorbia cheirolepis Fisch. & C.A. Mey.	Central Asia, *Vasák s.n.* (NY)	AF537424	—
Euphorbia chersonesa Huft	Mexico, Baja California Sur, *Steinmann 1252* (RSA)	AF537436	AF538174
Euphorbia clava Jacq.	Cultivated (nat. Republic of S. Africa), *Steinmann 1472-B* (RSA)	AF537569	AF538245
Euphorbia colletiodes Benth.	Mexico, Sonora, *Steinmann 93-387* (ARIZ)	AF537405	—
Euphorbia comosa Vell.	Brazil, *Webster 25425* (DAV)	AF537503	AF538222
Euphorbia crossadenia Pax & K. Hoffm.	Brazil, *Graças et al. 886* (SP)	AF537451	—
Euphorbia crotonoides Boiss.	Tanzania, *M.R. 23765* (NY)	AF537578	AF538238
Euphorbia delicatula Boiss.	Mexico, Guerrero, *Steinmann 1199* (RSA)	AF537393	AF538152

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia dendroides L.	Greece, *Strid 25582* (RSA)	AF537539	—
Euphorbia denisii Oudejans	Cultivated (nat. Madagascar), *Steinmann 1434* (RSA)	AF537497	—
Euphorbia depauperata Hochst. ex A. Rich.	Malawi, *Kaunda & Tawakali 906* (NY)	AF537556	—
Euphorbia discolor Ledeb.	Former U.S.S.R., *McNeal 710* (RSA)	AF537547	—
Euphorbia drupifera Thonn.	Cultivated (nat. Africa), *Steinmann 1488* (RSA)	AF537480	AF538191
Euphorbia eanophylla Croizat	Bolivia, *Beck 11399* (DAV)	AF537498	—
Euphorbia eglandulosa V.W. Steinm.	Mexico, Chiapas, *Breedlove 70137* (CAS)	AF537394	—
Euphorbia elata Brandegee	Brazil, *Daly 6694* (NY)	AF537495	AF538217
Euphorbia elliotii Leandri	Madagascar, *Dorr et al. 3985* (MO)	AF537478	—
Euphorbia epiphylloides Kurz	Cultivated (nat. Andaman Islands), *Steinmann 1459* (RSA)	AF537484	—
Euphorbia equisetiformis A. Stewart	Ecuador, Galapagos Islands, *Eliason & Eliason 1573* (K)	AF537388	—
Euphorbia eremophila A. Cunn.	Australia, *Vasek 680914-51* (RSA)	AF537423	—
Euphorbia eriantha Benth.	U.S.A., Arizona, *Steinmann 925* (RSA)	AF537440	AF538167
Euphorbia esculenta Marloth	Cultivated (nat. Republic of S. Africa), *Steinmann 1474* (RSA)	AF537575	—
Euphorbia espinosa Pax	Cultivated (nat. Africa), *Steinmann 1494* (RSA)	AF537416	AF538190
Euphorbia esula L.	U.S.A., New Jersey (nat. Eurasia), *Steinmann 1427* (RSA)	AF537546	AF538229
Euphorbia exstipulata Engelm.	U.S.A., Arizona, *Steinmann 934* (RSA)	AF537433	AF538171
Euphorbia fulgens Karw. ex Klotzsch	Mexico, Oaxaca, *Campos 813* (RSA)	AF537404	AF538154
Euphorbia gentryi V.W. Steinm. & T.F. Daniel	Mexico, Sonora, *Steinmann 94-357* (ARIZ)	AF537406	—
Euphorbia germainii Phil.	Chile, *Teillier 4267* (SGO)	AF537499	AF538205
Euphorbia geroldii Rauh	Cultivated (nat. Madagascar), *Steinmann 1467* (RSA)	AF537475	—
Euphorbia glanduligera Pax	Namibia, *Koutnik 2015* (DAV)	AF537426	AF538178
Euphorbia globosa (Haw.) Sims	Cultivated (nat. Republic of S. Africa), *Steinmann 1454-A* (RSA)	—	AF538239
Euphorbia goetzei Pax	Tanzania, *Taylor et al. 8490* (MO)	AF537413	AF538185
Euphorbia gollmeriana Klotzsch ex Boiss.	Venezuela, *Ramírez 2696* (DAV)	AF537501	AF538220
Euphorbia gottlebei Rauh	Cultivated (nat. Madagascar), *Steinmann 1471* (RSA)	AF537459	—
Euphorbia gradyi V.W. Steinm. & A. Ram.-Roa	Mexico, Oaxaca, *Steinmann 784* (RSA)	AF537407	AF538151
Euphorbia graminea Jacq.	Mexico, Sonora, *Steinmann 94-107* (RSA)	AF537410	AF538155
Euphorbia grantii Oliv.	Tanzania, *Bidgood et al. 1186* (MO)	—	AF538242
Euphorbia gregaria Marloth	Cultivated (nat. Republic of S. Africa), *Steinmann 1445-B* (RSA)	AF537527	—
Euphorbia guatemalensis Standl. & Steyerm.	Mexico, Chiapas, *Steinmann 1170* (RSA)	AF537408	—
Euphorbia guerichiana Pax	Republic of South Africa, *Balkwill et al. 6022* (MO)	AF537415	AF538182
Euphorbia gymnoclada Boiss.	Brazil, *Webster 25853* (DAV)	AF537456	—
Euphorbia gymnonota Urb.	Bahama Islands, *Correll & Wasshausen 46769* (NY)	AF537507	—

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia haeleeleana D.R. Herbst	U.S.A., Hawaii, *Fernstemacher s.n.* (NY)	AF537514	AF538206
Euphorbia hallii R.A. Dyer	Cultivated (nat. Republic of S. Africa), *Steinmann 1475* (RSA)	AF537573	—
Euphorbia hamata (Haw.) Sweet	Cultivated (nat. Republic of S. Africa), *Steinmann 1454-B* (RSA)	—	AF538237
Euphorbia hedyotoides N.E. Br.	Cultivated (nat. Madagascar), *Steinmann 1472-A* (RSA)	AF537460	AF538196
Euphorbia heterodoxa Müll. Arg.	Brazil, *Webster 25810* (DAV)	AF537500	—
Euphorbia heterophylla L.	Mexico, Sonora, *Van Devender 98-1157* (ARIZ)	AF537429	AF538170
Euphorbia hoffmanniana (Klotzsch & Garcke) Boiss.	Costa Rica, *Haber 10501* (F)	AF537508	AF538211
Euphorbia hormorhiza Radcl.-Sm.	Mexico, Tamaulipas, *Mayfield & Patterson 1843* (TEX)	AF537431	AF538165
Euphorbia iharanae Rauh	Cultivated (nat. Madagascar), *Steinmann 1458* (RSA)	AF537477	—
Euphorbia innocua L.C. Wheeler	U.S.A., Texas, *Mayfield 2168* (RSA)	AF537380	AF538161
Euphorbia insulana Vell.	Brazil, *Hora 03* (NY)	AF537411	—
Euphorbia ipecacuanhae L.	U.S.A., South Carolina, *Spongberg & Boufford 1718* (MO)	AF537397	—
Euphorbia jaliscensis B.L. Rob. & Greenm.	Mexico, Jalisco, *Steinmann 754* (RSA)	AF537442	AF538166
Euphorbia juttae Dinter	Cultivated (nat. Namibia), *Steinmann 1493* (RSA)	AF537418	AF538188
Euphorbia kraussiana Bernh.	Republic of S. Africa, *Stalmans 372* (MO)	AF537548	—
Euphorbia lacera Boiss.	Mexico. E. de Mexico, *Castilla & Tejero 958* (ENCB)	AF537441	—
Euphorbia lactiflua Phil.	Chile, *Dillon & Teillier 5105* (F)	AF537528	AF538219
Euphorbia lagunensis Huft	Mexico, Baja California Sur, *Steinmann 1272* (RSA)	AF537379	—
Euphorbia lagunillarum Croiz.	Cultivated (Venezuela), *Steinmann 1621* (RSA)	AF537502	—
Euphorbia lathyris L.	U.S.A., California (nat. Eurasia), *Steinmann 1426* (RSA)	AF537550	—
Euphorbia laurifolia Juss.	Ecuador, *Mena C61* (NY)	AF537509	—
Euphorbia leucocephala Lotsy	Cultivated (nat. Guatemala), *Steinmann 94-17* (RSA)	AF537381	—
Euphorbia lignosa Marloth	Cultivated (nat. Namibia), *Steinmann 1455* (RSA)	—	AF538240
Euphorbia longifolia Lam.	Canary Islands, *Lægaard 9905* (DAV)	AF537558	AF538235
Euphorbia longituberculosa Boiss.	Cultivated (nat. east tropical Africa), *Steinmann 1479* (RSA)	AF537577	AF538252
Euphorbia macropus (Klotzsch & Garcke) Boiss.	Mexico, Nuevo León, *Mayfield 1294* (TEX)	AF537378	—
Euphorbia macvaughii Carvajal & Lomelí	Cultivated (nat. Mexico, Michoacán), *Steinmann 1486* (RSA)	AF537382	—
Euphorbia mahabobokensis Rauh	Cultivated (nat. Madagascar), *Steinmann 1456* (RSA)	AF537522	—
Euphorbia matabelensis Pax	Botswana, *Smith 4229* (MO)	—	AF538247
Euphorbia mauritanica L.	Cultivated (nat. southern Africa), *Steinmann 1432* (RSA)	AF537531	—
Euphorbia medicaginea Boiss.	Morocco, *Podlech 41883* (RSA)	AF537535	—
Euphorbia meenae S. Carter	India, *Singh s.n.* (RSA)	AF537483	AF538202

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia megalatlantica Ball	Morocco, *Podlech 41177* (RSA)	AF537536	AF538226
Euphorbia meloformis Aiton	Cultivated (nat. Republic of S. Africa), *Steinmann 1490* (RSA)	AF537565	—
Euphorbia meuleniana O. Schwartz	Cultivated (nat. Yemen), *Steinmann 1448* (RSA)	AF537572	—
Euphorbia milii Des Moul.	Cultivated (nat. Madagascar), *Steinmann 1476* (RSA)	AF537461	AF538195
Euphorbia millotii Ursch & Leandri	Cultivated (nat. Madagascar), *Steinmann 1477* (RSA)	AF537463	—
Euphorbia misella S. Watson	Mexico, Chihuahua, *Steinmann 1032* (RSA)	AF537384	AF538160
Euphorbia misera Benth.	Mexico, Baja California, *Steinmann 1285* (RSA)	AF537383	—
Euphorbia monteiri Hook.f.	Botswana, *Long & Rae 290* (K)	AF537563	—
Euphorbia myrsinites L.	U.S.A., Colorado (nat. Eurasia), *Steinmann 1430* (RSA)	AF537551	AF538231
Euphorbia namuskluftensis L.C. Leach	Cultivated (nat. Namibia), *Steinmann 1491* (RSA)	AF537562	—
Euphorbia oaxacana B.L. Rob. & Greenm.	Mexico, Colima, *Steinmann 1094* (RSA)	AF537373	—
Euphorbia obesa Hook.f.	Cultivated (nat. Republic of S. Africa), *Steinmann 1465* (RSA)	AF537566	AF538244
Euphorbia oblongata Griseb.	U.S.A., California (nat. Europe), *Halse 4334* (RSA)	AF537555	—
Euphorbia ocymoidea L.	Mexico, Jalisco, *Steinmann 1139* (RSA)	AF537392	—
Euphorbia oerstediana (Klotzsch & Garcke) Boiss.	U.S.A., Puerto Rico, *Axelrod & Sastre 6278* (NY)	—	AF538159
Euphorbia omariana M.G. Gilbert	Ethiopia, *Friss et al. 3674* (K)	AF537560	AF538243
Euphorbia panchganiensis Blatt. & McCann	India, *Singh s.n.* (RSA)	AF537375	—
Euphorbia papillosa A. St.-Hil.	Argentina, *Renvoize 3068* (RSA)	AF537510	—
Euphorbia pedilanthoides Denis	Cultivated (nat. Madagascar), *Steinmann 1438* (RSA)	—	AF538192
Euphorbia pentadactyla Griseb.	Argentina, *Cantino 700* (ARIZ)	AF537428	—
Euphorbia peperomioides Boiss.	Brazil, *Nakjima et al. 1596* (DAV)	AF537523	—
Euphorbia peplus L.	U.S.A., California (nat. Eurasia), *Steinmann 1433* (RSA)	AF537532	AF538228
Euphorbia perrieri Drake	Cultivated (nat. Madagascar), *Steinmann 1483* (RSA)	AF537463	—
Euphorbia pervilleana Baill.	Cultivated (nat. Madagascar), *Steinmann 1444* (RSA)	AF537518	AF538209
Euphorbia petiolata Banks & Sol.	Middle East, *Liston 7-85-388/3* (RSA)	AF537422	AF538180
Euphorbia phosphorea Mart.	Cultivated (nat. Brazil), *Steinmann 1446* (RSA)	AF537512	AF538223
Euphorbia phylloclada Boiss.	Republic of S. Africa, *Oliver et al. 6611* (K)	AF537427	AF538179
Euphorbia pilosa L.	Former U.S.S.R., *Elias et al. 7182* (RSA)	AF537557	AF538234
Euphorbia pirottae N. Terrac.	Cultivated (nat. Tanzania), *Steinmann 1440* (RSA)	AF537417	AF538186
Euphorbia platycephala Pax	Tanzania, *Bidgood et al. 2249* (K)	AF537561	AF538241
Euphorbia platyclada Rauh	Cultivated (nat. Madagascar), *Steinmann 1447* (RSA)	AF537421	AF538187
Euphorbia plumerioides Teijsm. ex Hassk.	Australia, *Fryxell & Craven 4022* (RSA)	AF537513	—

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Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia poissonii Pax	Cultivated (west tropical Africa), *Steinmann 1498* (RSA)	AF537482	AF538193
Euphorbia polyantha Pax	Kenya, *Faden & Faden 74/477* (K)	—	AF538189
Euphorbia primulifolia Baker	Cultivated (nat. Madagascar), *Steinmann 1484* (RSA)	AF537466	—
Euphorbia pteroneura A. Berger (1)	Mexico, Chiapas, *Mayfield 980* (TEX)	AF537506	AF538210
Euphorbia pteroneura A. Berger (2)	Cultivated (nat. Mexico/Cent. America), *Steinmann 1622* (RSA)	AF537505	—
Euphorbia pteroneura A. Berger (3)	Cultivated (nat. Mexico/Cent. America), *Steinmann 1623* (RSA)	AF537504	—
Euphorbia pulcherrima Willd. ex Klotzsch	Mexico, Nayarit, *Steinmann 1070* (RSA)	AF537432	AF538168
Euphorbia pumicola Huft	Mexico, Baja California Sur, *Steinmann 1241* (ARIZ)	AF537437	AF538164
Euphorbia punicea Sw.	Cultivated (nat. Jamaica), *Raz 193* (NY)	AF537516	AF538208
Euphorbia radians Benth.	Mexico, Sonora, *Steinmann 944* (RSA)	AF537438	AF538169
Euphorbia regis-jubae Webb & Berthel.	Cultivated (nat. Canary Islands), *Steinmann 1431* (RSA)	AF537541	—
Euphorbia rhombifolia Boiss.	Cultivated (nat. Republic of S. Africa), *Steinmann 1439* (RSA)	AF537414	AF538183
Euphorbia robusta (Engelm.) Small	U.S.A., Colorado, *Steinmann 1429* (RSA)	AF537533	AF538227
Euphorbia rossiana Pax	Mexico, Puebla, *Steinmann 1195* (RSA)	AF537374	—
Euphorbia rossiana var. nov.	Mexico, Guerrero, *Steinmann 1199* (RSA)	AF537390	—
Euphorbia rossii Rauh & Buchloh	Cultivated (nat. Madagascar), *Steinmann 1449* (RSA)	AF537465	—
Euphorbia rubella Pax	Cultivated (nat. east tropical Africa), *Steinmann 1464* (RSA)	AF537487	AF538204
Euphorbia rzedowskii McVaugh	Mexico, Michoacán, *Steinmann 1110* (RSA)	AF537399	—
Euphorbia sarcodes Boiss.	Brazil, *Cordeiro et al. 2233* (SP)	AF537454	—
Euphorbia scatorhiza S. Carter	Cultivated (nat. Somalia), *Steinmann 1441* (RSA)	AF537420	AF538181
Euphorbia scheffleri Pax	Cultivated (nat. Kenya), *Steinmann 1452* (RSA)	—	AF538249
Euphorbia schimperi Presl	Cultivated (nat. Arabian Peninsula/NE tropical Africa), *Steinmann 1499* (RSA)	AF537537	—
Euphorbia sessilifolia Klotzsch ex Boiss. (1)	Brazil, *Arbo 5418* (DAV)	AF537453	—
Euphorbia sessilifolia Klotzsch ex. Boiss. (2)	Brazil, *Cordeiro et al. 2218* (SP)	AF537452	—
Euphorbia segoviensis (Klotzsch & Garcke) Boiss.	Mexico, Chiapas, *Steinmann 1174* (RSA)	AF537400	—
Euphorbia sinaloensis Brandegee	Mexico, Sonora, *Steinmann 94-130* (ARIZ)	AF537401	AF538156
Euphorbia sipolisii N.E. Br.	Cultivated (nat. Brazil), *Steinmann 1443* (RSA)	AF537517	—
Euphorbia socotrana Balf.f.	Cultivated (nat. Socotra), *Steinmann 1436* (RSA)	—	AF538248
Euphorbia sonorae Rose	Mexico, Sonora, *Steinmann 964* (RSA)	AF537402	—
Euphorbia soongarica Boiss.	Former U.S.S.R., *Elias 9850* (RSA)	AF537545	—
Euphorbia spathulata Lam.	U.S.A., California, *Banks 1601* (RSA)	AF537552	AF538233
Euphorbia sphaerorhiza Benth.	Mexico, Sonora, *Steinmann 1020* (RSA)	AF537412	AF538158

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Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Euphorbia stenophylla (Klotzsch & Garcke) Boiss.	Brazil, *Aparecida da Silva & dos Santos 3267* (DAV)	AF537529	—
Euphorbia stricta L.	Austria, *Wallnofer 8531* (NY)	AF537559	—
Euphorbia strigosa Hook. & Arn.	Mexico, Nayarit, *Steinmann 1079* (RSA)	AF537439	AF538163
Euphorbia subpeltata S. Watson	Mexico, Morelos, *Steinmann 794* (RSA)	AF537376	—
Euphorbia succedanea L.C. Wheeler	Mexico, Aguascalientes, *Steinmann 745* (RSA)	AF537403	AF538162
Euphorbia tannensis Spreng.	Australia, *Fryxell et al. 4475* (RSA)	AF537425	AF538184
Euphorbia tanquahuete Sessé & Mociño	Cultivated (Mexico), *Steinmann 1620* (RSA)	AF537525	AF538224
Euphorbia teke Schweinf. ex Pax	Cultivated (nat. east tropical Africa), *Steinmann 1470* (RSA)	AF537485	—
Euphorbia tetraptera Baker	Madagascar, *Rabevohita 2093* (DAV)	AF537526	—
Euphorbia thinophila Phil.	Chile, *Dillon & Teillier 5127* (F)	AF537530	AF538218
Euphorbia thouarsiana Baill.	Madagascar, *Leeuwenburg & Ranaivojaona 14585* (K)	AF537474	—
Euphorbia tirucalli L.	Cultivated (nat. Africa/Madagascar), *Steinmann 1445-A* (RSA)	AF537479	—
Euphorbia trichadenia Pax	Cultivated (nat. Zimbabwe/Angola), *Steinmann 1461* (RSA)	AF537564	AF538236
Euphorbia trichotoma HBK	Belize, *Hill 20357* (MO)	AF537534	—
Euphorbia tuberosa L.	Cultivated (nat. Republic of S. Africa), *Steinmann 1472-C* (RSA)	AF537570	AF538246
Euphorbia tubiglans Marloth ex R.A. Dyer	Cultivated (nat. Republic of S. Africa), *Steinmann 1462* (RSA)	AF537567	—
Euphorbia turczaninowii Kar. & Kir.	China, *Liston 827-4* (RSA)	AF537543	—
Euphorbia usambarica Pax	Tanzania, *Balsler 291* (NY)	AF537538	—
Euphorbia weberbaueri Mansf.	Cultivated (nat. Peru), *Steinmann 1347* (RSA)	AF537519	AF538212
Euphorbia whitei L.C. Wheeler	Mexico, Oaxaca, *Torres 10833* (DAV)	AF537391	—
Euphorbia zonosperma Müll.Arg.	Brazil, *Plowman et al. 8579* (F)	AF537430	—
Euphorbia xylophylloides Brongn. ex Lem.	Cultivated (nat. Madagascar), *Steinmann 1450* (RSA)	AF537467	AF538214
Euphorbia sp.	Cultivated (nat. probably Africa), *Steinmann 1469* (RSA)	AF537481	—
Euphorbia sp. nov. 1	Brazil, *Coredeiro et al. 2203* (SP)	AF537457	—
Euphorbia sp. nov. 2	Mexico, Tamaulipas, *Mayfield 1851* (TEX)	—	AF538157
Monadenium elegans S. Carter	Cultivated (nat. Tanzania), *Steinmann 1473-A* (RSA)	AF537470	AF538199
Monadenium ellenbeckii N.E. Br.	Cultivated (nat. east tropical Africa), *Steinmann 1453* (RSA)	—	AF538200
Monadenium lindenii S. Carter	Cultivated (nat. Somalia), *Steinmann 1485* (RSA)	AF537473	—
Monadenium magnificum E.A. Bruce	Cultivated (nat. Tanzania), *Steinmann 1496* (RSA)	AF537472	—
Pedilanthus bracteatus Jacq.	Cultivated (nat. Mexico), *Steinmann 1460* (RSA)	AF537489	—
Pedilanthus calcaratus Schltdl.	Mexico, Veracruz, *Cházaro B. & de Cházaro 7294* (NY)	AF537492	—
Pedilanthus connatus Dressler & Sacamano	Mexico, Jalisco, *Sacamano s.n.* (MO)	AF537493	—
Pedilanthus cymbiferus Schltdl.	Mexico, Puebla, *Steinmann 1624* (RSA)	AF537491	—

Appendix 1. Continued.

Taxon	Origin and voucher	ITS GenBank accession	*ndh*F GenBank accession
Pedilanthus finkii Boiss.	Mexico, Oaxaca, *Meave del Castillo 1551* (MO)	AF537520	—
Pedilanthus macrocarpus Benth.	Mexico, Baja California, *Steinmann 1235* (RSA)	AF537490	—
Pedilanthus tehuacanus Brandegee	Mexico, Puebla, *Steinmann 1400* (RSA)	AF537488	AF538215
Pedilanthus tithymaloides (L.) Poit.	Guatemala, *Castillo 2713* (NY)	AF537494	AF538216
Synadenium grantii Hook.f.	Cultivated (east tropical Africa), *Steinmann 1497* (RSA)	AF537469	AF538201

MOLECULAR PHYLOGENETICS AND MORPHOLOGICAL EVOLUTION IN CUNONIEAE (CUNONIACEAE)[1]

Jason C. Bradford[2]

Abstract

The Cunonieae are the largest tribe in the flowering plant family Cunoniaceae and include the widespread genus *Weinmannia*. This study aims to understand phylogenetic relationships within Cunonieae by using DNA sequences in a parsimony-cladistic analysis. Sequenced loci included the internal transcribed spacers (ITS-1 and ITS-2) of nuclear ribosomal DNA, and the *trn*L intron and *trn*L-F spacer of chloroplast DNA. Primer and taxon-specific amplification of non-orthologous ITS-2 copies made it necessary to exclude the ITS-2 data, but otherwise the nuclear and chloroplast data sets were congruent. The results place *Vesselowskya* as the sister genus to other Cunonieae and support the monophyly of *Pancheria*, *Cunonia*, and all five sections of *Weinmannia*, but do not indicate how these groups are related. The monophyly of *Weinmannia* sect. *Weinmannia* is upheld, with *W. trichosperma* from temperate forests of South America and *W. tinctoria* from the Mascarene Islands placed basal to a large clade of tropical American species. Although morphological data maintain the monophyly of *Weinmannia*, this is neither verified nor statistically refuted by the molecular data. Likewise, *Cunonia*, with one isolated South African species, has only weak molecular support but clear morphological synapomorphies. Lack of support for relationships among major clades within Cunonieae makes it difficult to suggest patterns of morphological evolution. However, a well-supported phylogenetic hypothesis within *Weinmannia* sect. *Leiospermum* is used to discuss heterotopy in inflorescence architecture. Uniquely derived features of the inflorescence are found in the New Caledonian species *Weinmannia dichotoma* and in the New Zealand species *W. silvicola* and *W. racemosa*. These heterotopic changes involve alternate patterns in the fate of terminal meristems and the arrangement of metamers bearing racemes. In an appendix the correct orthographies and original publications of all five sections of *Weinmannia* are provided; types are also designated for *Weinmannia* sections *Inspersae* and *Spicatae* in order to validate them.

Key words: cladistics, *Cunonia*, Cunoniaceae, Cunonieae, evolution, *Fasciculatae*, heterotopy, inflorescence architecture, *Inspersae*, ITS, *Leiospermum*, molecular systematics, *Pancheria*, paralogous loci, *Spicatae*, *trn*F, *trn*L, *Vesselowskya*, *Weinmannia*.

The flowering plant family Cunoniaceae R. Br. (Oxalidales) (Angiosperm Phylogeny Group, 1998) comprises about 300 species in 26 genera. Plants of the family are trees and shrubs in wet tropical and cool temperate forests, with most genera occurring in eastern Australia, Melanesia, and New Guinea. About 210 Cunoniaceae species are in a monophyletic group of four genera called the tribe Cunonieae (Bradford & Barnes, 2001). *Weinmannia* is by far the largest and most widely distributed genus, with over 150 species found in the Americas, islands of the eastern Indian Ocean, Malesia, and the South Pacific (Bradford, 1998; Hopkins, 1998a). *Weinmannia* is divided into five sections, with each one largely restricted to a particular geographic region. The Cunonieae are also composed of the two other largest genera in Cunoniaceae, *Pancheria*, with about 30 species endemic to New Caledonia (Guillaumin, 1940; Morat, 1993), and *Cunonia*, with about 25 species in New Caledonia and 1 species in the South African Cape region (Hoogland et al., 1997). *Vesselowskya*, the remaining genus in the tribe, has only two species endemic to eastern Australia (Rozefelds et al., 2001).

A few recent publications have provided new insights on the taxonomy and phylogeny of Cunon-

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ieae. In a study of the relationship between *Weinmannia* and its putative close relative, *Cunonia*, using a cladistic analysis of morphological features (Bradford, 1998) there was weak support for the monophyly of *Weinmannia*, four of its sections, and of *Cunonia*. A family-level analysis by Bradford and Barnes (2001) based on morphology and chloroplast DNA sequences (*rbc*L and *trn*L-*trn*F) established a new tribal classification, and clarified generic circumscriptions by proposing apomorphic morphological characters for each genus.

Several recent generic revisions have provided valuable details on taxonomic distribution and morphology for many Cunonieae species. Rozefelds et al. (2001) gave a table summarizing similarities and differences among genera of Cunonieae and described a new species of *Vesselowskya*. New species descriptions and keys have also been produced for *Cunonia* (Hoogland et al., 1997) and Malagasy *Weinmannia* (Bradford, 2001; Bradford & Miller, 2001). Revisions have been completed for *Weinmannia* of Malesia and the South Pacific (Hopkins, 1998a, b, c; Hopkins & Florence, 1998). *Weinmannia* of the Americas are poorly studied in their entirety, although some national and regional treatments have been done (Harling, 1999; Bradford & Berry, 1998).

Despite these efforts, relationships among Cunonieae genera are unclear, the monophyly of *Weinmannia* is in doubt, and the monophyly of some sections within *Weinmannia* is poorly established. In this study, I use DNA sequences from chloroplast and nuclear loci to clarify phylogenetic relationships within Cunonieae. In addition, I show that the phylogenetic hypotheses generated by this molecular data can help reevaluate character evolution within the tribe, especially with respect to inflorescence architecture.

Methods

Based on the family-level analysis of Bradford and Barnes (2001), Cunonieae are clearly monophyletic, and taxon sampling was designed to maximize the geographic, phylogenetic, and morphological diversity within this clade that has been elucidated by previous studies (Bradford, 1998). One distinctive species endemic to Sulawesi, *Weinmannia descombesiana*, is missing; otherwise, sampling is broad, including exemplars from 45 species of Cunonieae (Table 1). Codieae may be the most closely related tribe to Cunonieae, but I was unable to obtain internal transcribed spacer (ITS) nrDNA sequences of Codieae to use as outgroups. Instead, ITS trees were rooted using two species from another closely related tribe, Caldcluvieae (Bradford & Barnes, 2001). The *trn*L-*trn*F cpDNA (Taberlet et al., 1991) data set uses several outgroup taxa from closely related tribes.

Collections were made from native populations and botanical gardens between 1994 and 1998. Fresh leaves were dried in silica gel for DNA preservation. All DNA samples are vouchered with herbarium specimens and were deposited at MO and in the country of origin. Table 1 lists source and voucher information of each herbarium specimen and GenBank accession numbers for all DNA sequences. Detailed information is available for Bradford collections on the TROPICOS database (⟨http://www.mobot.org⟩).

I sequenced both the nuclear ITS region (Baldwin, 1992) and two adjacent chloroplast loci, the *trn*L intron and the intergenic spacer between the *trn*L 3′ exon and *trn*F (Taberlet et al., 1991). The ITS region was sequenced first, which helped establish likely monophyletic groups. A smaller set of *trn*L-*trn*F sequences was obtained from a subsample of each distinct lineage that was discerned from ITS data. Standard methods were used to extract, amplify, and sequence DNA loci, and these are described in Bradford and Barnes (2001). BLAST (⟨http://www.ncbi.nlm.nih.gov/BLAST/⟩) comparisons were done to confirm that sequences were of angiosperm origin and not from possible fungal or other contaminants, and indeed similar nucleotide sequences were of appropriate loci and within the eudicot clade.

Standard ITS primers (Baldwin, 1992) did not strongly amplify or produce clear sequences of ITS-2 for many species in *Weinmannia* sections *Leiospermum* and *Inspersae*, or in *Pancheria*, *Geissois*, and *Caldcluvia*. Hypothesizing that high G-C content was interfering with PCR amplification, I designed alternative primers with higher annealing temperatures based on published sequences of 26S rDNA (Kuzoff et al., 1998) and 5.8 rDNA sequences from my own work. The new primers did yield clear sequences as hoped, but preliminary cladistic analysis using ITS-2 data alone resolved clades with a mixture of ingroups and outgroups, a result incongruent with ITS-1, chloroplast, and morphological data (see Bradford, 2000, chapter 1, for a figure of these results). This suggested that the ITS-2 region amplified using the new primers was not orthologous to ITS-1 sequences obtained using the standard (e.g., ITS4) primers. To test this, a Partition Homogeneity Test (PAUP*4.0b6a; Swofford, 2001) was used to compare the ITS-1 and ITS-2 data sets, and they were found to be significantly incongruent (500 replicates, $P = 0.002$). Because

ITS-1 and ITS-2 are adjacent loci they should have the same evolutionary history; significant incongruence between them strongly suggests that non-orthologous loci were amplified. The ITS region is known to contain multiple copies of the ribosomal genes, as well as pseudogenes, and different PCR conditions can preferentially amplify different paralogous loci (Buckler et al., 1997). Until the issue of paralogy can be resolved, the decision was made to exclude the ITS-2 data from analyses of organismal phylogeny; these sequences, however, are available in GenBank (phylogenetic data set with the range AF521255–AF521298).

Sequences were aligned by eye in Se-Al (Rambaut, 1995) and exported in a NEXUS format. Insertions and deletions were scored as binary characters (e.g., present or absent). Any regions with ambiguous sequence or uncertain alignment were ignored during analysis. Parsimony cladistic analyses were implemented in PAUP*4.0b6a (Swofford, 2001). For all parsimony analyses, the following options were used: characters unweighted and unordered, searches heuristic, starting trees obtained via random stepwise addition, TBR branch swapping, COLLAPSE option on, STEEPEST DESCENT option off, MULTREES on. Support for clades was estimated with bootstrap values (using the "Fast" bootstrap option with 10,000 replicates in PAUP) and decay values (using Autodecay; Eriksson, 1999).

The nuclear and chloroplast data sets were combined after checking for compatibility using the Partition Homogeneity Test in PAUP. This test could not reject the null hypothesis that the data sets represent the same evolutionary history (500 replicates, $P = 0.06$).

Results

ITS-1 analysis

The final ITS-1 data set included 48 sequences from 47 species (45 in Cunonieae) and a matrix of 260 characters. The number of equally parsimonious trees found during heuristic searches made it impossible to complete branch swapping. Several searches were done using random taxon addition, and each analysis found the same large tree island with 268 steps (CI = 0.70, RI = 0.86). The strict consensus of this tree island shown in Figure 1 is based on over 30,000 equally parsimonious trees.

The ITS-1 data strongly support the sister-group relationship between *Vesselowskya* and the rest of Cunonieae (Fig. 1). *Pancheria* is monophyletic and weakly placed as the sister to clades of *Weinmannia* and *Cunonia*. Five traditionally recognized groups are resolved as clades, including *Cunonia*, and four sections of *Weinmannia*: sects. *Weinmannia*, *Inspersae*, *Spicatae*, and *Fasciculatae*. Species from *Weinmannia* sect. *Leiospermum* form part of a large polytomy. The two sections from Madagascar, section *Inspersae* and section *Spicatae*, are placed as sister taxa to each other. Not all of these clades have high "Fast" bootstrap values, however, and the data give no support for relationships between these larger clades.

*trn*L-F analysis

The *trn*L-F data set included 996 characters from sequences representing 38 species (29 in Cunonieae). Ingroup sampling was less intensive than with the ITS data set, but included sufficient sampling from all major ITS clades. The parsimony analysis found 420 trees of 244 steps (CI = 0.73, RI = 0.82) (Fig. 2).

On the strict consensus tree, Cunonieae are monophyletic, and *Vesselowskya* is placed as the sister group to other Cunonieae. In contrast to ITS results, *Weinmannia* sect. *Weinmannia* is the sister taxon to a large clade containing *Cunonia*, *Pancheria*, and all other species of *Weinmannia*. *Cunonia capensis*, from South Africa, groups with *Pancheria* while other *Cunonia* are monophyletic and sister to the remaining *Weinmannia*. Malagasy *Weinmannia* (sects. *Inspersae* and *Spicatae)* form a clade, as do sections *Fasciculatae* and *Leiospermum*. The internal topology of the cladogram has low bootstrap values.

Combined analysis

For the combined analysis, 29 taxa, including 27 from the Cunonieae, were sequenced for both ITS and *trn*L-F. The final data set included 1254 characters. The parsimony analysis found a single most parsimonious tree of 388 steps (CI = 0.74, RI = 0.81) (Fig. 3).

The base of the tree is structured similar to the ITS trees: *Vesselowskya* is basal to all Cunoniae, and *Pancheria* is a sister taxon to the clade containing *Weinmannia* and *Cunonia*. Although there is strong support for the position of *Vesselowskya*, no other internal branches have high "Fast" bootstrap or decay values. High "Fast" bootstrap and decay values do support most of the commonly recognized taxa, including *Pancheria* and all five *Weinmannia* sections. By contrast, *Cunonia* does not form a clade in the "Fast" bootstrap consensus tree and has a decay value of one.

Table 1. Vouchers for exemplars used in DNA sequencing and the GenBank number of each sequence are given. Exemplars are organized by outgroups, Cunonieae, genera, and sections of *Weinmannia*. Based on recent revisions and work in progress, the best current estimates of the number of species in Cunonieae and its subtaxa are given.

Genus	Species (number of species in taxon)	Collection	Native origin (cultivated)	*trn*L c–d	*trn*L e–F	ITS1
OUTGROUPS						
Ackama	*paniculosa* (F. Muell.) Beuzev. & C. T. White	*Bradford 843* (MO, BRI)	Australia	AF299161	AF299214	
Ackama	*rosifolia* A. Cunn.	*Bradford 909* (MO, BRI)	New Zealand	AF299162	AF299215	
Caldcluvia	*paniculata* D. Don	*Barnes s.n.* (HO 516497)	Chile (Australia)	AF299163	AF299216	AF485640
Callicoma	*serratifolia* Andrews	*Bradford 857* (MO, NSW)	Australia	AF299170	AF299223	
Codia	*discolor* Guillaumin	*Bradford 600* (MO, NOU)	New Caledonia	AF299171	AF299224	
Geissois	*benthamiana* F. Muell.	*Bradford 859* (MO, BRI)	Australia	AF299165	AF299218	
Geissois	*superba* Gillespie	*Hopkins 5019* (MO, SUVA)	Fiji			
Pullea	cf. *glabra* Schltr.	*Bradford 585* (MO, SUVA)	Fiji	AF299172	AF299225	
Spiraeopsis	*celebica* Blume	*Bradford 840* (MO, BSIP)	Solomon Islands	AF299164	AF299217	AF485641
CUNONIEAE R. Br. (210)						
Cunonia L. (26)						
Cunonia	*atrorubens* Schltr.	*Bradford 614* (MO, NOU)	New Caledonia	AF299154	AF299207	AF485628
Cunonia	*balansae* Brongn. & Gris.	*Bradford 617* (MO, NOU)	New Caledonia	AF299155	AF299208	AF485629
Cunonia	*capensis* L.	*Bradford 735* (MO)	South Africa (U.S.)	AF299156	AF299209	AF485630
Cunonia	*macrophylla* Brongn. & Gris	*Bradford 607* (MO, NOU)	New Caledonia	AF299157	AF299210	AF485631
Cunonia	*montana* Schltr.	*Bradford 609* (MO, NOU)	New Caledonia			AF485632
Cunonia	*pulchella* Brongn. & Gris	*Bradford 635* (MO, NOU)	New Caledonia			AF485633
Pancheria Brongn. & Gris (30)						
Pancheria	*brunhessii* Pampan.	*Bradford 616* (MO, NOU)	New Caledonia			AF485634
Pancheria	*engleriana* Schltr.	*Bradford 602* (MO, NOU)	New Caledonia	AF299158	AF299211	AF485635
Pancheria	*hirsuta* Vieill. ex Pampan.	*Bradford 610* (MO, NOU)	New Caledonia	AF299159	AF299212	AF485636
Pancheria	*phylliraeoides* Brongn. & Gris ex Guillaumin	*Bradford 620* (MO, NOU)	New Caledonia			AF485637
Pancheria	*reticulata* Guillaumin	*Bradford 618* (MO, NOU)	New Caledonia			AF485638
Vesselowskya Pamp. (2)						
Vesselowskya	*venusta* Rozefelds, R. W. Barnes & Pellow	*Bradford 879* (MO, NSW)	Australia	AF299160	AF299213	AF485639
Weinmannia L. (151)						
section *Leiospermum* D. Don (22)						
Weinmannia	*dichotoma* Brongn. & Gris	*Hopkins 5053* (MO, NOU)	New Caledonia	AF299142	AF299195	AF485595
Weinmannia	*parviflora* G. Forst.	*Bradford 914* (MO, PAP)	Society Islands			AF485596
Weinmannia	*racemosa* L. f.	*Bradford 936* (MO)	New Zealand (U.S.)			AF485597
Weinmannia	*raiatensis* J. W. Moore	*Bradford 927* (MO, PAP)	Society Islands	AF299141	AF299194	AF485598

Table 1. Continued.

Genus	Species (number of species in taxon)	Collection	Native origin (cultivated)	*trn*L c–d	*trn*L e–F	ITS1
Weinmannia	*samoensis* A. Gray	*Bradford 800* (MO)	Samoa	AF299143	AF299196	AF485599
Weinmannia	*silvicola* Sol. ex A. Cunn.	*Bradford 912* (MO, AKU)	New Zealand	AF299144	AF299197	AF485601
Weinmannia	*serrata* Brongn. & Gris	*Bradford 627* (MO, NOU)	New Caledonia			AF485600
Weinmannia	sp. nov. 1 (cf. Hopkins, 1998c)	*Bradford 837* (MO, BSIP)	Solomons			AF485594
Weinmannia	*vescoi* Drake	*Bradford 921* (MO, PAP)	Society Islands			AF485602
Weinmannia	*vitiensis* Seem.	*Hopkins 5041* (MO, P, SUVA)	Fiji			AF485603
section *Fasciculatae* Bernardi ex Hoogland & H. C. Hopkins (19)						
Weinmannia	*clemensiae* Steenis	*Hopkins 5011* (MO, KIN, P)	Malaysia	AF299147	AF299200	AF485612
Weinmannia	*exigua* A. C. Sm.	*Bradford 814* (MO, BSIP)	Solomons	AF299148	AF299201	AF485614
Weinmannia	*fraxinea* (1) Sm. ex D. Don	*Bradford 578* (MO, P, KEP)	Malaysia Peninsula	AF299149	AF299202	AF485613
Weinmannia	*fraxinea* (2) Sm. ex D. Don	*Hopkins 5001* (MO, SAN)	Borneo			AF485615
Weinmannia	*hooglandii* H. C. Hopkins & J. C. Bradford	*Bradford 579* (MO, P, KEP)	Malay Peninsula			AF485616
Weinmannia	*richii* A. Gray	*Hopkins 5023* (MO, P, SUVA)	Fiji			AF485617
section *Spicatae* Bernardi ex. J. C. Bradford (26)						
Weinmannia	*arguta* (Bernardi) J. C. Bradford	*Bradford 642* (MO, TAN)	Madagascar			AF485618
Weinmannia	*bojeriana* Tul.	*Bradford 639* (MO, TAN)	Madagascar			AF485619
Weinmannia	*humbertiana* Bernardi	*Bradford 695* (MO, TAN)	Madagascar			AF485620
Weinmannia	*marojejyensis* J. S. Mill. & J. S. Bradford	*Bradford 692* (MO, TAN)	Madagascar			AF485621
Weinmannia	*minutiflora* Baker	*Malcomber 2874* (MO, TAN)	Madagascar	AF299150	AF299203	AF485622
Weinmannia	*sanguisugarum* Bernardi	*Bradford 715* (MO, TAN)	Madagascar	AF299151	AF299204	AF485623
Weinmannia	*stenostachya* Baker	*Bradford 650* (MO, TAN)	Madagascar			AF485624
section *Inspersae* Bernardi ex J. C. Bradford (9)						
Weinmannia	*madagascariensis* DC. ex Ser.	*Bradford 653b* (MO, TAN)	Madagascar	AF299152	AF299205	AF485626
Weinmannia	*rutenbergii* Engl.	*Malcomber 2880* (MO, TAN)	Madagascar	AF299153	AF299206	AF485627
Weinmannia	sp. nov. 2	*Bradford 655* (MO, TAN)	Madagascar			AF485625
section *Weinmannia* L. (77)						
Weinmannia	*auriculata* Hieron.	*Bradford 547* (MO, USZ)	Bolivia			AF485605
Weinmannia	*bangii* Rusby	*Bradford 525* (MO, USZ)	Bolivia	AF299145	AF299198	AF485606
Weinmannia	*ellantantha* Diels	*Bradford 538* (MO, USZ)	Bolivia			AF485607
Weinmannia	*myrtifolia* Cuatrec.	*Bradford 745* (MO, COL)	Colombia			AF485608
Weinmannia	sp. nov. 3	*Bradford 435* (MO, PORT)	Venezuela			AF485604
Weinmannia	*tinctoria* Sm.	*D'Argent, s.n.* (MAU 22790)	Mauritius	AF299146	AF299199	AF485609
Weinmannia	*tomentosa* L. f.	*Bradford 751* (MO, COL)	Colombia			AF485610
Weinmannia	*trichosperma* Cav.	*Bradford 738* (MO)	Chile (U.S.)			AF485611

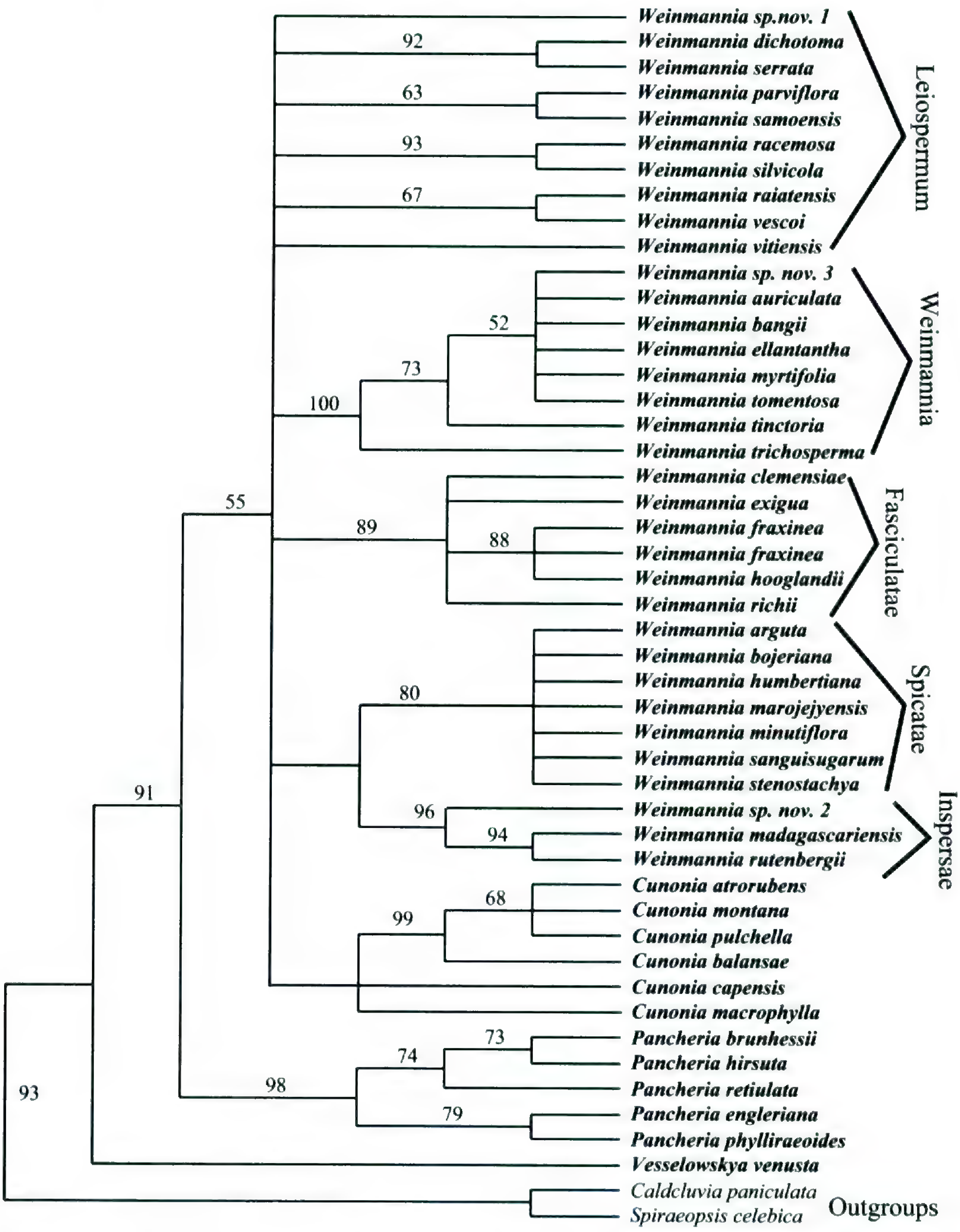

Figure 1. Strict consensus of >30,000 most parsimonious trees of ITS-1 sequences. "Fast" bootstrap values are above branches. Each section of *Weinmannia* is labeled to the right of the tree.

Discussion

In several respects, the phylogeny of the Cunoniae resulting from the combined analysis of ITS and *trn*L-F (Fig. 3) is highly congruent with previously published studies using morphological characters (Bradford, 1998). It differs primarily by showing that *Weinmannia* sect. *Weinmannia* is not nested within section *Fasciculatae*. Most significantly, the combined data support the monophyly of *Pancheria*, *Cunonia* (albeit weakly), and all five sections of *Weinmannia*. This analysis also suggests that Malagasy taxa form a clade. Although the combined data set does produce a highly resolved tree, "Fast" bootstrap and decay analyses do not give much support for internal nodes, indicating that relationships between major clades within Cunonieae are still poorly understood.

In contrast to the results of Bradford (1998), the molecular data sets do not uphold the monophyly

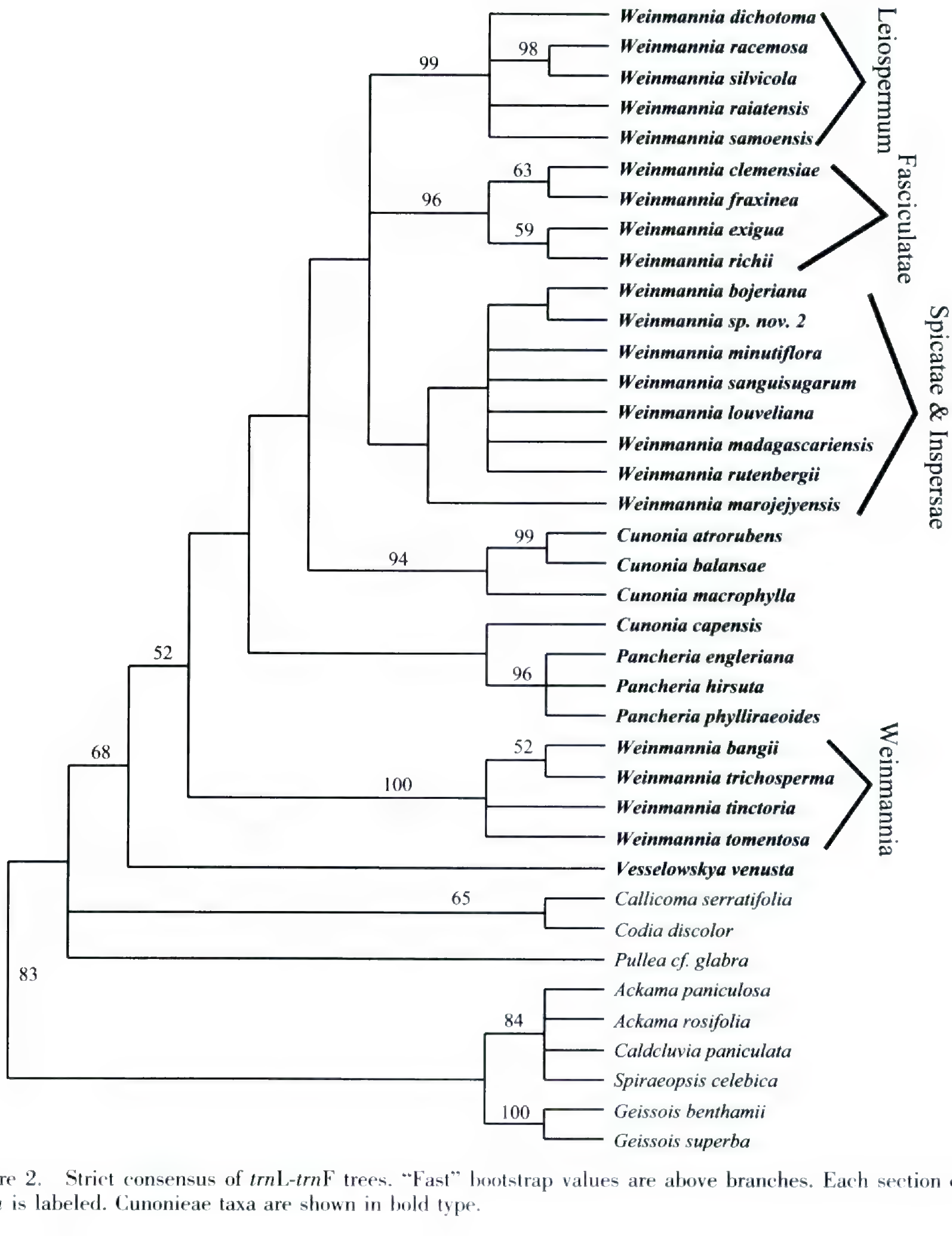

Figure 2. Strict consensus of *trn*L-*trn*F trees. "Fast" bootstrap values are above branches. Each section of *Weinmannia* is labeled. Cunonieae taxa are shown in bold type.

of *Weinmannia*. *Weinmannia* sect. *Weinmannia* has a very long branch and is placed as a sister group to *Cunonia* and other *Weinmannia* (Fig. 3). This long branch and the short internal nodes make it possible that these results are not dependable. To test whether this data set could statistically reject the hypothesis of a monophyletic *Weinmannia*, I built a constraint tree in MacClade (Maddison & Maddison, 1992) making *Weinmannia* monophyletic and enforced this topology in PAUP while reanalyzing the combined data set. A single tree of 390 steps was found, only one step more than the tree found in the unconstrained analysis. A Wilcoxon signed-rank test was then used to compare the most parsimonious tree with the monophyletic *Weinmannia* tree (Templeton, 1983; Mason-Gamer & Kellogg, 1996), and the null hypothesis of a monophyletic *Weinmannia* could not be rejected ($N = 3$, $T = 2$, $P = 0.56$). It would therefore be premature to consider *Weinmannia* paraphyletic based on this data.

Morphologically, *Weinmannia* is recognized easily by the presence of hairs on the seeds, which are lacking in other Cunonieae. Also, *Pancheria*, *Cunonia*, and *Vesselowskya* have winged seeds, but wings are lacking in *Weinmannia*. To account for

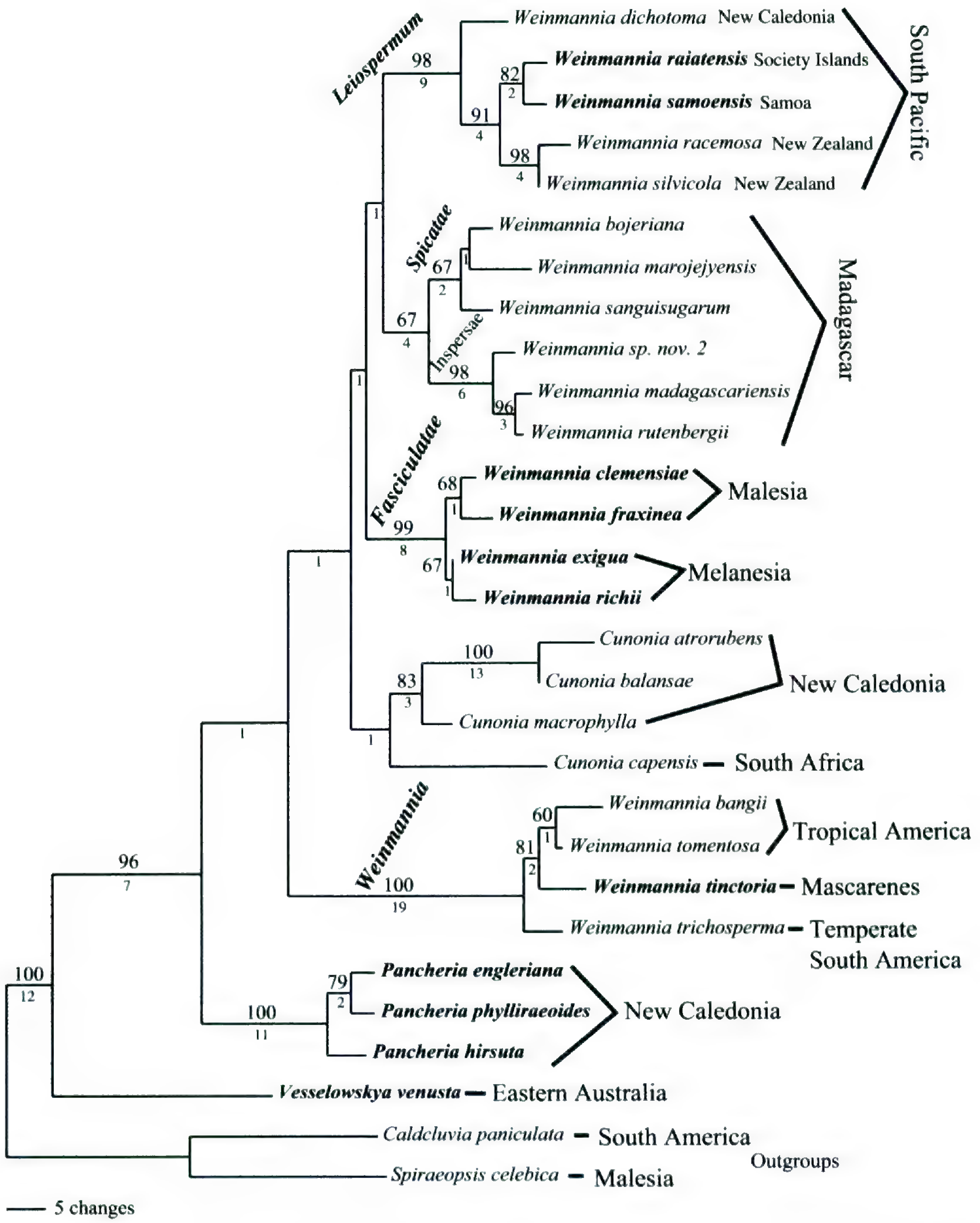

Figure 3. Phylogram of the single most parsimonious tree from the combined analysis. "Fast" bootstrap values are given above branches, decay values below. The clades corresponding to each section of *Weinmannia* are labeled, as is the geographic occurrence of species. Species placed in bold type have a dioecious breeding system; others are monoecious, usually with bisexual flowers.

these character states with a paraphyletic *Weinmannia*, two additional morphological steps are required: either seed hairs were gained twice and seed wings were lost twice (once on each of the two *Weinmannia* lineages), or a reversal of both characters occurred in *Cunonia* (Fig. 4). Other characters supporting the monophyly of *Weinmannia* have been found in micromorphological studies by R. Barnes (see Bradford & Barnes, 2001) in which multicellular hair bases were found in all sections of *Weinmannia*, but not in every species. These kinds of hairs have never been found in other genera of Cunoniaceae.

Although combined molecular data provide little

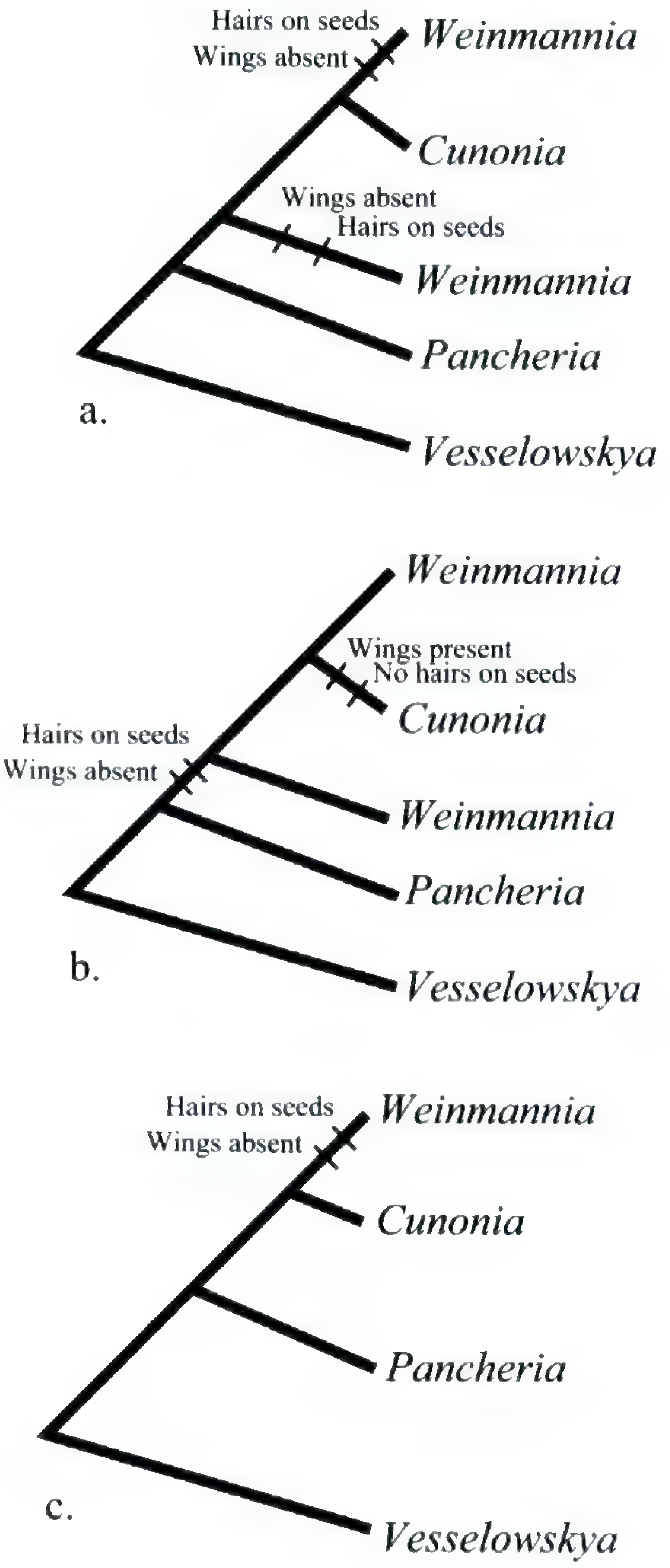

Figure 4. Alternative hypotheses for relationships within Cunonieae. —a & b. *Weinmannia* is paraphyletic with respect to *Cunonia*. This involves 389 steps in the combined molecular data set, and 4 more morphological ones. —c. *Weinmannia* is monophyletic. This involves 390 steps in the combined molecular data set, and 2 more morphological ones.

support for the cladistic relationships among *Pancheria*, *Cunonia*, and *Weinmannia* sections, new insights into relationships within genera and sections have emerged.

The South African species *Cunonia capensis* was recognized by Bradford (1998) as being morphologically similar to two very distinctive New Caledonian species, *C. macrophylla* and *C. schinziana*. All three species have larger flowers and fruits than other *Cunonia*, and similar inflorescence architectures composed of axillary pairs of stout racemes at the ends of stems. This inflorescence architecture is more reduced than the compound racemes typically found in other *Cunonia* (Hoogland et al., 1997). Morphological cladistic analyses showed this group of species to be a highly derived clade within *Cunonia*. In contrast, the combined molecular data make *Cunonia capensis* basal within *Cunonia*, and *C. macrophylla* basal within New Caledonian *Cunonia* (Fig. 3).

Most Cunoniaceae, including Cunonieae, are pollinated by small flying insects, especially bees. The distinctive features of *Cunonia capensis* and *C. macrophylla* may be due to their unusual pollination biology. Observations show their visitors include nectar-feeding birds that perch at the base of the raceme (Hopkins, pers. obs.; Coates Palgrave, 1983), which makes sense considering their relatively large flowers and simple, rigid inflorescence structure. The combined cladogram (Fig. 3) suggests that similarities between *Cunonia capensis* and *Cunonia macrophylla* may be plesiomorphic. Given that bird pollination is only known in one other Cunoniaceae genus (*Geissois*), it seems unlikely that bird-pollination was plesiomorphic during the origin of *Cunonia*, although it may be for the extant clade. Alternatively, bird pollination may be convergent in *Cunonia capensis* and *C. macrophylla*, but testing these hypotheses for ancient lineages is nearly impossible.

Although molecular systematics only gives weak support to the monophyly of *Cunonia*, the genus is morphologically distinct. At least two characters are shared only by species of *Cunonia*: fruits that have a circumbasal-acropetal dehiscence, a character unique in the family, and floral disks that are adnate to the base of the ovary, unlike any other Cunonieae (Bradford, 1998; Bradford & Barnes, 2001; Rozefelds et al., 2001).

The most well-supported clade in the analyses is that of *Weinmannia* sect. *Weinmannia*. This is the largest section in the genus and is disjunct between the Americas, where over 70 species occur, and the Mascarene Islands, where 2 species are endemic. The Mascarene species are distinguished by being dioecious, but otherwise are similar to American species (Bradford, 1998). Although the topology is not strongly supported, Mascarene species, represented here by *Weinmannia tinctoria*, are nested between *W. trichosperma*, from temperate forests of South America, and a clade of species from Neotropical montane forests.

Weinmannia trichosperma is apparently a remnant of a more ancient, temperate lineage within *Weinmannia* sect. *Weinmannia*—a lineage that macrofossils show may have once occurred in Tasmania as well (Carpenter & Buchanan, 1993). That a derived tropical clade of the section is disjunct between the neotropics and the Mascarenes suggests that interchange across the Atlantic and In-

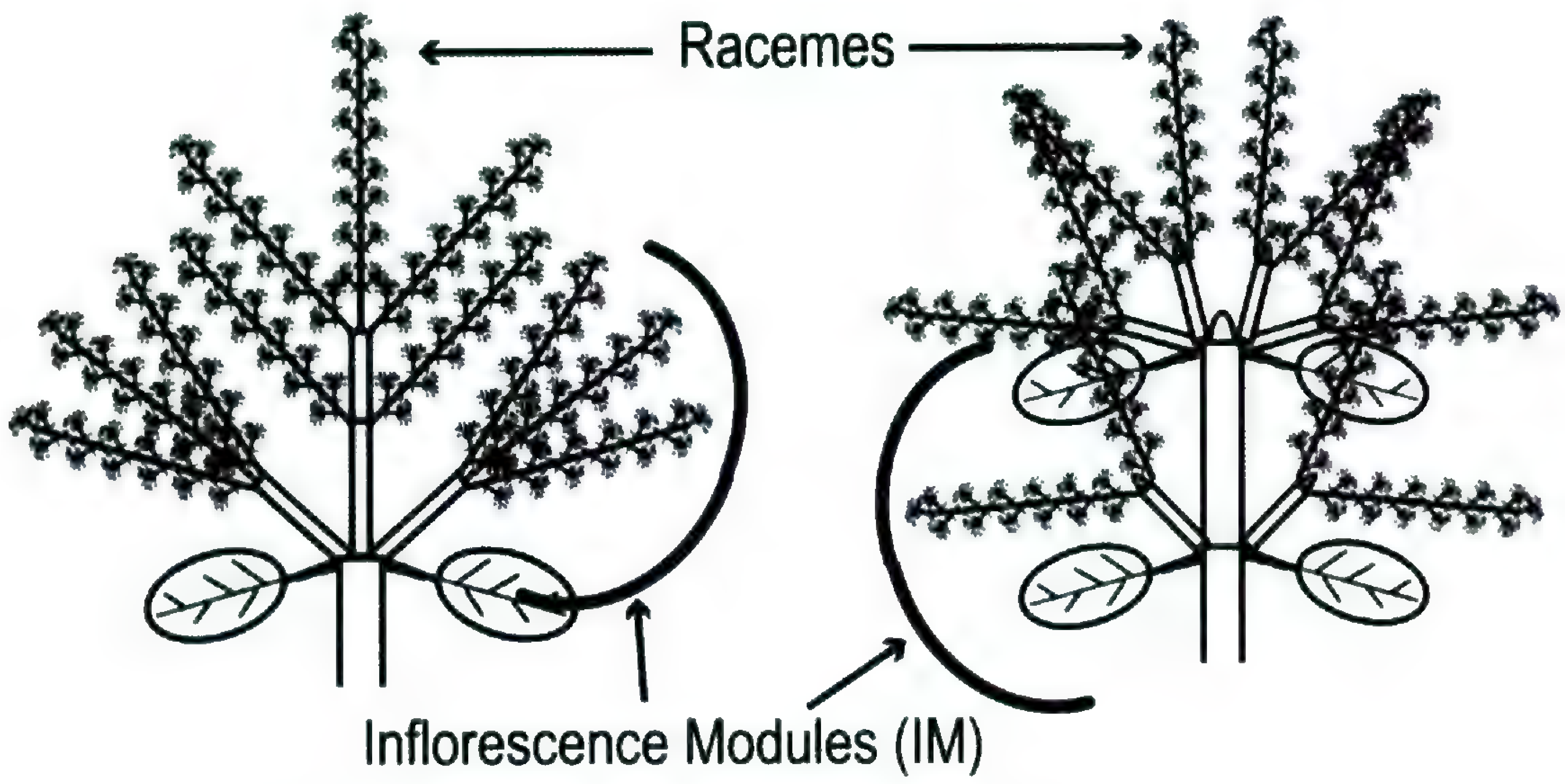

Figure 5. Two common inflorescence architectures in *Weinmannia* are shown; left, section *Leiospermum;* right, section *Fasciculatae*. Racemes, internodes, and meristems are organized in particular patterns to form higher order units called Inflorescence Modules (IMs), and IMs are organized in particular patterns along the main stem to comprise the Total Inflorescence.

dian Oceans has occurred more recently than interchange between temperate and tropical America. However, since only a few molecular characters support this unexpected relationship, additional data are required to test it.

In Bradford (1998), *Weinmannia* sect. *Fasciculatae* was paraphyletic with respect to a highly derived *Weinmannia* sect. *Weinmannia*. This view is overturned by the molecular evidence. *Weinmannia* sect. *Fasciculatae* has high bootstrap and decay values (Figs. 2–4). Missing from this study, however, is sequence data for *Weinmannia descombesiana*, an unusual species placed in section *Fasciculatae*, but with some traits suggestive of section *Leiospermum* (Hopkins, 1998b).

Weinmannia sect. *Leiospermum* is widely distributed in the South Pacific, from the Bismarcks to the Marquesas, and from Rapa to New Zealand (Hopkins, 1998a, 1998c; Hopkins & Florence, 1998). Bradford (1998) recognized three species groups within the section: New Caledonian species, New Zealand species, and other South Pacific species. The two species from New Zealand, *Weinmannia racemosa* and *W. silvicola*, each have distinctive and unique inflorescence architectures. South Pacific species outside of New Caledonia are dioecious. As a whole, New Caledonian species have no obviously derived features; however, *Weinmannia dichotoma* aborts its terminal meristem at every node. Although each individual data set is ambiguous, the combined analysis strongly supports the monophyly of section *Leiospermum* and places the New Caledonian clade sister to clades from the South Pacific and New Zealand (Fig. 3).

A well-supported phylogeny presents an opportunity to reevaluate some of the morphological characters I discussed in previous studies (Bradford, 1998). This earlier work emphasized inflorescence architecture and heterotopy, and some background on this is warranted here. The inflorescence in Cunonieae comprises nested sets of structures. The most familiar of these are the flower-bearing axes, raceme-like in most genera, but ball-shaped in *Pancheria* (Rozefelds et al., 2001). These flower-bearing axes, along with internodes and meristems, are typically arranged in repeated units I term Inflorescence Modules (IMs) (Fig. 5). The structure of IMs and their arrangement is highly variable among Cunonieae genera and *Weinmannia* sections (Fig. 6). This observation led to a system of coding inflorescence architecture based on principles of positional homology (see Bradford, 1998, for details).

Molecular systematics has confirmed the general perception from comparative morphology that inflorescence evolution represents heterotopy, and that these characters can be effectively coded for morphological cladistic analyses. For example, phylogenetic support for some clades in the morphological cladistic analysis was based mainly on these characters. The monophyly of *Weinmannia* sect. *Leiospermum* was supported by two characters of the inflorescence: having a sequential arrangement of metamers within an IM, and having the largest IMs in the terminal (i.e., acrotonic) position (Figs. 5, 6, 7).

Furthermore, improved support for clades within section *Leiospermum* can be used to make specific statements about the pattern of heterotopic changes. From the generalized inflorescence form of section *Leiospermum* (see top and bottom left diagrams

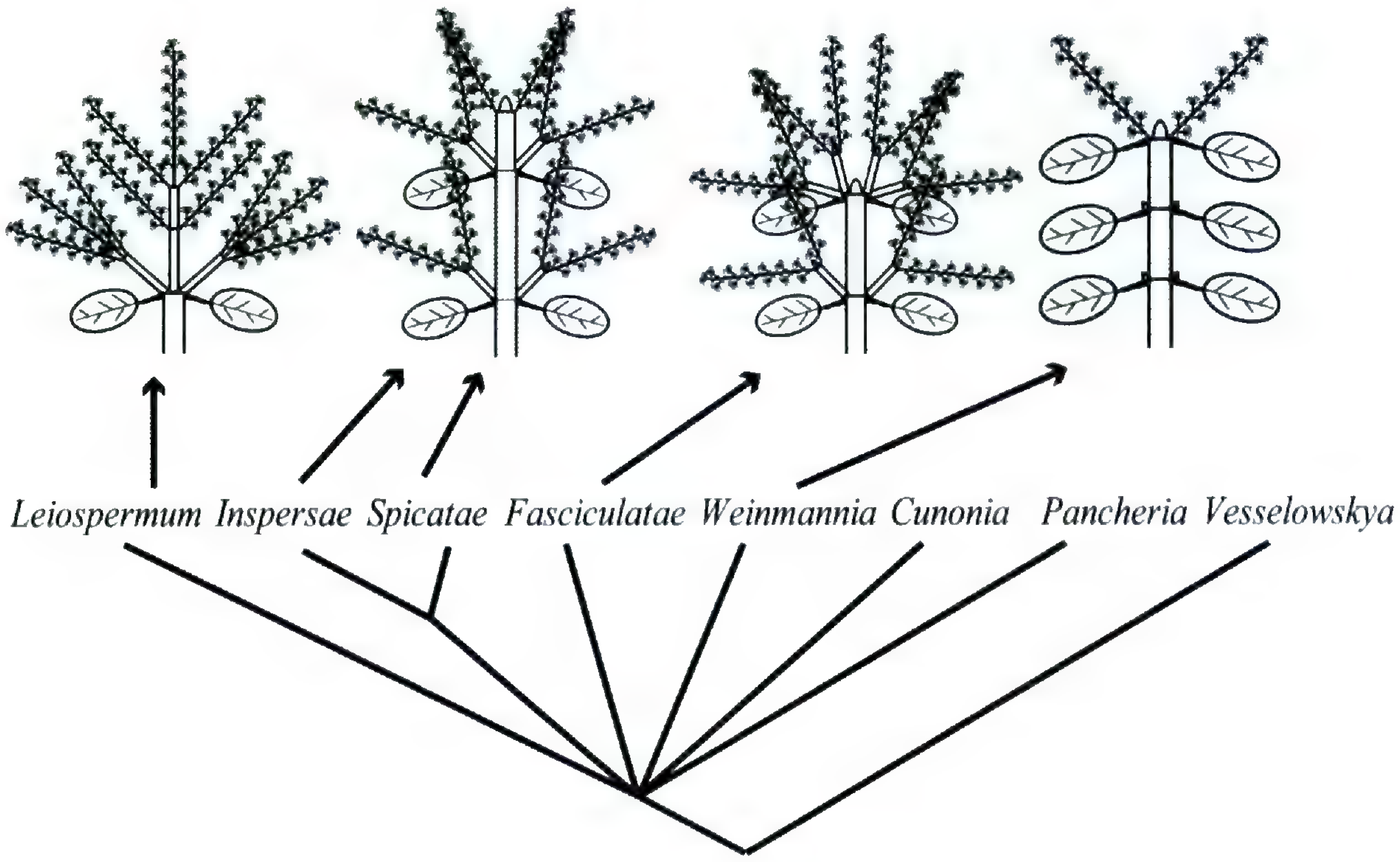

Figure 6. The general breadth of inflorescence diversity in *Weinmannia* is illustrated and linked to taxonomy and phylogeny. The phylogeny is based upon Figure 3, but clades having no bootstrap support and a decay value of only 1 were collapsed. *Cunonia* and *Pancheria* inflorescences are typically similar to sections *Inspersae* and *Spicatae*, although *C. macrophylla* and *C. capensis* are similar to section *Weinmannia*. *Vesselowskya* inflorescences display similarities to both sections *Fasciculatae* and *Leiospermum*. For detailed illustrations of inflorescence diversity in Cunonieae see Bradford (1998, 2001), Hoogland et al. (1997), the publication series of Hopkins (1998), and Rozefelds et al. (2001).

of Fig. 7), it is clear that species from New Zealand (*Weinmannia racemosa* and *W. silvicola*) have derived heterotopic changes in their inflorescences (see right diagrams of Fig. 7). *Weinmannia racemosa* has regained vegetative growth beyond the inflorescence with a terminal vegetative bud, a reversal to the plesiomorphic state found in other sections of *Weinmannia* (Fig. 6). This species has also lost the development of lateral inflorescence modules. The other species from New Zealand, *Weinmannia silvicola*, has developmental asymmetry; although it does not always produce lateral IMs, when present, they develop only from one axillary bud. Furthermore, *Weinmannia silvicola* is the only species to produce sequential metamers within an IM and then abort the apical meristem. Other species, such as *Weinmannia dichotoma* from New Caledonia (see left diagram in Fig. 7), abort the apical meristem at the first metamer within an IM. Although abortion of the apical meristem occurs as part of normal variation among IMs within many *Weinmannia* plants in the South Pacific, the fixation of this trait is apparently derived within *Weinmannia dichotoma*. (See also Hopkins, 1998a, 1998c; Hopkins & Florence, 1998.)

Without a more resolved phylogeny it is difficult to re-evaluate other characters discussed previously (Bradford, 1998), such as dioecy. Although the strong phylogenetic hypothesis for *Weinmannia* sect. *Leiospermum* indicates that dioecy evolved once within this clade (Fig. 3), it is difficult to discern the general pattern of breeding system evolution within Cunonieae (see also Bradford, 1998; Rozefelds et al., 2001).

Conclusions

Molecular systematics has enabled us to confidently delineate some major lineages within Cunonieae and provided sufficient resolution in some clades to re-examine inflorescence evolution. Unfortunately, little is known still about how Cunonieae genera and *Weinmannia* sections relate, except for the basal position of *Vesselowskya* (Fig. 6). Until a better phylogenetic hypothesis is available, it is best to retain the genera as currently circumscribed, despite questions about the monophyly of *Weinmannia*. Remaining to be addressed is character evolution for many traits that vary among genera of Cunonieae and sections of *Weinmannia*, although evolution within some genera and sections has been clarified.

This work is the first in-depth attempt to understand the phylogeny of Cunonieae. While taxon sampling was broad, the number of sequenced loci was likely insufficient to resolve all nodes. Ques-

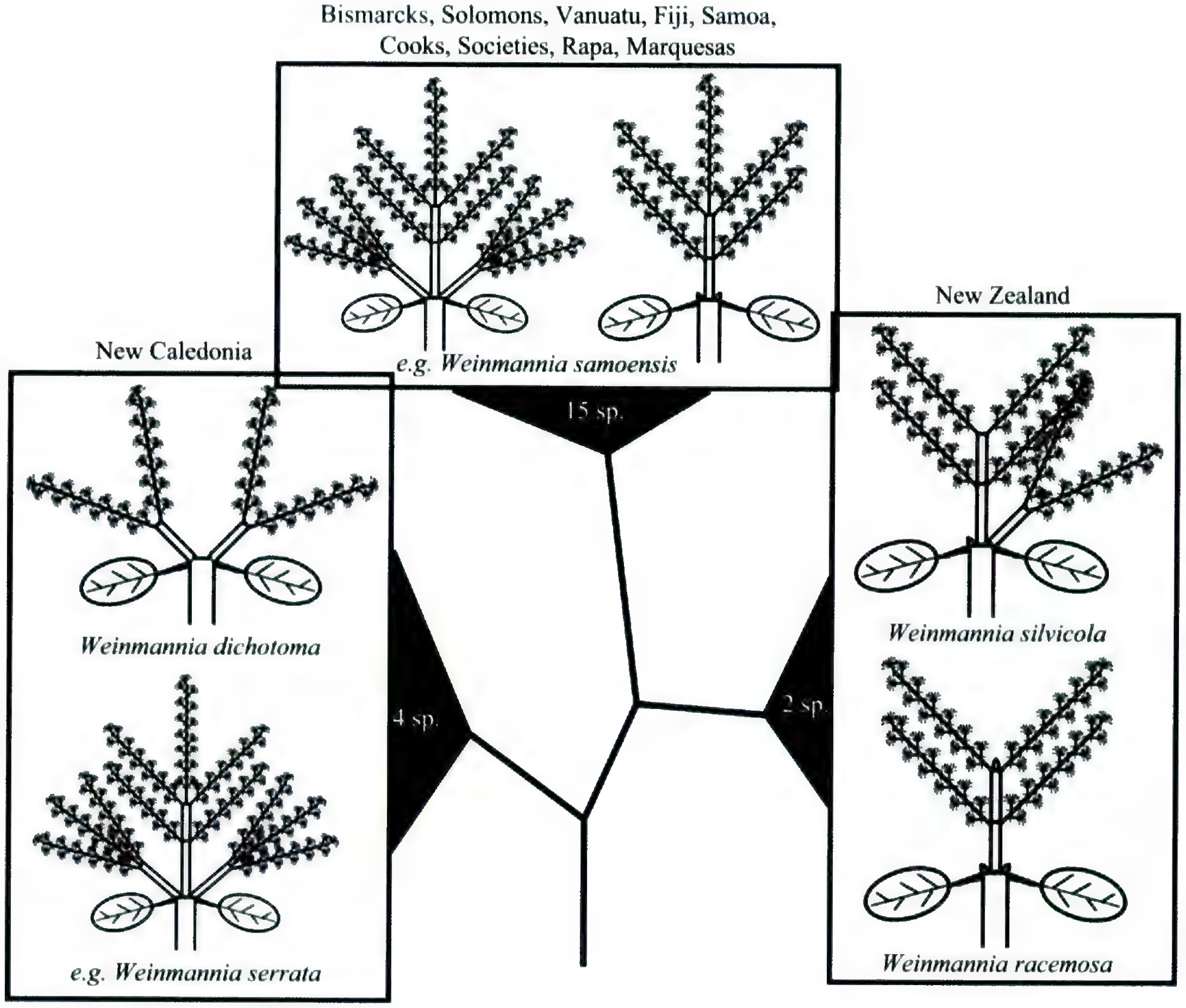

Figure 7. Relationships among clades within *Weinmannia* sect. *Leiospermum* based on the analyses presented here. The number of species and location of each clade is labeled. Some common forms of inflorescence architecture are shown, and the most unusual species, *Weinmannia silvicola*, *W. racemosa*, and *W. dichotoma*, are highlighted.

tions about character evolution may best be studied by comparing variation within species, sections, and genera rather than at the tribal level. For example, Malagasy *Weinmannia* have the richest variety of inflorescence architecture, sympatric *Cunonia* species have a diversity of floral coloration and scents, and in many *Weinmannia* species from Malesia and the South Pacific dioecy is "leaky" with morphologically male, female, and bisexual flowers found within a single population or plant. Most importantly, studies on the spatial ecology of species are almost totally lacking and would be useful for effective conservation measures.

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Appendix 1

The following are correct orthographies (following Greuter et al., 2000, ICBN Art. 21.2) and original publications of all five sections of *Weinmannia.* Types are also designated here for two sections.

Weinmannia L., Syst. Nat., ed. 10, 2: 997, 1005, 1367. 1759, nom. cons. TYPE: *Weinmannia pinnata* L.

Weinmannia sect. *Simplicifoliae* Bernardi, Candollea 18: 289. 1963, nom. invalid., sine typo.

Weinmannia sect. **Leiospermum** (D. Don) Engl., Nat. Pflanzenfam. 3 (2a): 101. 1891. *Leiospermum* D. Don, Edinburgh New Philos. J. 9: 91. 1830. TYPE: *Weinmannia racemosa* L.f., Suppl. 227. 1781. (lectotype, designated by H. C. Hopkins, 1998a: 21).

Weinmannia sect. *Racemosae* Bernardi, Bot. Jahrb. Syst. 83: 132, 185. 1964.

Weinmannia sect. **Fasciculatae** Bernardi ex Hoogland & H. C. Hopkins, Adansonia, sér. 3: 21. 1998. TYPE: *Weinmannia fraxinea* (D. Don) Miq.

Weinmannia sect. **Inspersae** Bernardi ex J. C. Bradford, **sect. nov.** *Weinmannia* sect. *Inspersae* Bernardi, Bot. Jahrb. Syst. 83: 132, 143. 1964, nom. invalid., sine typo. TYPE: *Weinmannia madagascariensis* DC. This section was originally published without a type species.

Weinmannia sect. **Spicatae** Bernardi ex J. C. Bradford, **sect. nov.** *Weinmannia* sect. *Spicatae* Bernardi, Bot. Jahrb. Syst. 83: 132. 1964, nom. invalid., sine typo. TYPE: *Weinmannia bojeriana* Tul. This section was originally published without a type species.

CONTRIBUCIÓN A LA FILOGENIA DEL GÉNERO *PASPALUM* (POACEAE: PANICOIDEAE: PANICEAE)[1]

Sandra S. Aliscioni[2]

Resumen

El género *Paspalum* L. presenta alrededor de 330 especies y una amplia distribución geográfica, principalmente en las regiones tropicales y subtropicales de América. Debido a la marcada variabilidad morfológica entre sus especies, diversos autores intentaron dividir al género en subgéneros, secciones o grupos informales de especies. En el presente trabajo se realizó un análisis cladístico del género *Paspalum* utilizando caracteres anatómicos foliares y exomorfológicos con la finalidad de poner a prueba su origen monofilético y establecer relaciones filogenéticas entre las especies más representativas. Asimismo se analizó el grado de homoplasia de los caracteres con el objeto de estimar su valor diagnóstico y calidad informativa en la caracterización de los distintos grupos. Para el análisis cladístico se consideraron 47 especies pertenecientes a 27 grupos establecidos según Chase con algunas modificaciones propuestas por Cialdella et al. y Morrone et al. Se identificaron 36 caracteres exomorfológicos y anatómicos foliares. La matriz de datos fue analizada bajo el criterio de parsimonia con pesos iguales y con pesado implícito de caracteres utilizando los programas Nona y Pee-Wee respectivamente. Sobre la base de los caracteres utilizados en este análisis no pudo establecerse un origen común para el género confirmándose que el mismo representa una asociación parafilética de especies, estrechamente relacionadas con *Axonopus* P. Beauv. y *Thrasya* Kunth, géneros también pertenecientes a la tribu Paniceae.

Abstract

Paspalum L. has approximately 330 species and a large geographical distribution, mainly in tropical and subtropical regions of America. Due to the morphological variability among the species, different authors have proposed dividing the genus into subgenera, sections, or informal groups. A cladistic analysis of *Paspalum* was conducted using anatomical foliar and exomorphological characters to test its monophyly and its phylogenetic relationships among representative species. The degree of character homoplasy was analyzed in order to estimate the diagnostic value of anatomical characters among groups. For the cladistic analysis, 47 species of 27 groups established by Chase, with modification established by Cialdella et al. and Morrone et al., and 36 exomorphological and anatomical foliar characters were considered. The data matrix was analyzed with Nona and Pee-Wee, parsimony programs using equal weights and implied weighting. The present phylogenetic analysis confirms that *Paspalum* is a paraphyletic group and shows close relationships with *Axonopus* and *Thrasya* in Paniceae.

Key words: *Axonopus*, Paniceae, Panicoideae, *Paspalum*, Poaceae, *Thrasya*.

El género *Paspalum* L. es uno de los más importantes dentro de la tribu Paniceae debido al elevado número de especies que presenta y a su amplia distribución geográfica, habitando principalmente regiones tropicales y subtropicales de América, con pocas especies en África y Asia. La falta de un estudio taxonómico global para este género hace difícil estimar en la actualidad el número total de especies. Según Chase (1929) el mismo incluye aproximadamente 400 taxones; Clayton y Renvoize (1986) consideran que comprende alrededor de 330 especies.

La importancia económica del género radica en que muchas de sus especies son consideradas excelentes forrajeras naturales, como por ejemplo *P. notatum* Flüggé, "pasto horqueta" y *P. dilatatum* Poir., "pasto miel."

El género incluye hierbas perennes, rara vez anuales, cespitosas o rastreras, estoloníferas o rizomatosas. Se distingue de otros miembros de la tribu por presentar inflorescencias con racimos espiciformes unilaterales; articulación de la espiguilla en la base junto al pedicelo; espiguillas abaxiales, solitarias o apareadas, dispuestas en 2 a 4

[1] El presente trabajo constituye parte de la Tesis Doctoral presentada en la Facultad de Ciencias Naturales de la Universidad Nacional de La Plata. Expreso mi agradecimiento a mis directores, el Dr. F. Zuloaga y la Dra. M. Arriaga por todo el apoyo brindado y a mis compañeros L. Aagesen, L. Giussani y O. Morrone por las sugerencias aportadas y lectura crítica del manuscrito.

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hileras, dorsiventralmente comprimidas, plano-convexas o cóncavo-convexas; gluma inferior usualmente ausente y antecio superior endurecido obovoide a elipsoide (Chase, 1929; Burkart, 1969; Judziewicz, 1990).

Debido al elevado número de especies y a la marcada variabilidad morfológica entre las mismas, diversos autores han intentado dividir a *Paspalum* en subgéneros, secciones o grupos informales, detectándose dificultades para dicha delimitación. Estas categorías fueron establecidas sobre la base de caracteres exomorfológicos, principalmente a nivel de la espiguilla (pilosidad de la espiguilla, morfología de la gluma superior, textura y coloración del antecio, etc.) sin considerarse en la mayoría de los casos los caracteres anatómicos foliares. Los estudios taxonómicos llevados a cabo hasta el momento son fragmentarios: el género *Paspalum* ha sido tratado en revisiones parciales y floras regionales (Chase, 1927; Parodi, 1928, 1932, 1937; Hitchcock, 1951; Barreto, 1954, 1957, 1966, 1967; Burkart, 1969; Rosengurtt et al., 1970; Quarín, 1975; Sendulsky & Burman, 1978, 1980a, b; da Silva et al., 1979; Pohl, 1980; Smith et al., 1982; Renvoize, 1984, 1987a; Crins, 1991; Judziewicz, 1990; Filgueiras, 1993; Cialdella et al., 1995; Morrone et al., 1995, 1996, 2000; Rodriguez, 1998; Rodriguez et al., 2000). Cabe destacar el valioso aporte realizado por Chase (1929) al estudiar las especies de *Paspalum* que crecen en América del Norte, estableciendo 27 grupos de especies con un total de 140 taxones distribuidos en los mismos.

La anatomía foliar de *Paspalum* fue estudiada por Türpe (1967), quien describió detalladamente las características histofoliares de las especies argentinas sin aportar datos que permitan inferir relaciones entre ellas. Aliscioni y Arriaga (1998) llevaron a cabo un estudio anatómico comparado en los grupos Quadrifaria y Virgata del género *Paspalum*, destacando la semejanza anatómica entre ambos. Posteriormente, Aliscioni (1999) realizó un estudio histofoliar de las especies más representativas del género, observando que *Paspalum* es anatómicamente heterogéneo presentando caracteres diferenciales a nivel de especie o grupo de especies, algunos de los cuales mantienen cierta relación con los agrupamientos establecidos sobre la base de caracteres exomorfológicos. Por otro lado la autora muestra que los únicos caracteres anatómicos comunes a todas las especies estudiadas son aquellos asociados al tipo de vía fotosintética, los cuales permiten corroborar que el género presenta anatomía Kranz del subtipo MS, fisiológicamente C_4 NADP-me.

Türpe (1967) define a *Paspalum* como un género anatómicamente homogéneo y considera que los caracteres diferenciales que se pueden observar en las hojas, reflejan las condiciones ecológicas del medio en el cual habitan las especies. Sin embargo, Aliscioni (2000) estudió la anatomía ecológica de algunas especies de *Paspalum* y describió diferentes estrategias adaptativas presentes en el género destacando que especies de hábitats muy diferentes pueden manifestar características anatómicas similares.

Existen estudios filogenéticos realizados en la tribu Paniceae los cuales incluyen un escaso número de especies de *Paspalum*. Sobre la base de datos morfológicos, Zuloaga et al. (2000) no lograron resolver las relaciones dentro del género, mientras que Duvall et al. (2001) y Giussani et al. (2001) realizaron análisis moleculares concluyendo en ambos casos que *Paspalum* sería parafilético.

En el presente trabajo se realizó un análisis filogenético con el objeto de poner a prueba la monofilia de *Paspalum*. Se plantea una hipótesis sobre la historia evolutiva del género estableciendo posibles relaciones filogenéticas entre las especies más representativas. Asimismo se analiza el valor diagnóstico de los caracteres exomorfológicos y anatómicos a la luz de las relaciones filogenéticas, comparando el grado de homoplasia presente en cada uno de ellos con el objeto de evaluar su importancia en la caracterización de los distintos grupos de especies.

Materiales y Métodos

Selección del grupo interno

El análisis cladístico se realizó sobre la base de 47 especies correspondientes a 27 grupos informales de *Paspalum* establecidos según Chase (1929, inéd.) con modificaciones propuestas por Cialdella et al. (1995) para el grupo Bonplandiana y por Morrone et al. (1995, 1996) en los grupos Racemosa y Dissecta. Para seleccionar los taxones terminales se consideraron representantes de la mayoría de los grupos informales del género, tratando de abarcar la máxima variabilidad morfológica como así también cubrir el área de distribución geográfica que presenta el género en América. Se seleccionó una especie representativa de los grupos Conjugata, Dissecta, Gardneriana, Inaequivalvia, Macrophylla, Orbiculata y Saccharoidea, y dos especies para cada uno de los restantes grupos. Cuando estuvieron disponibles, se seleccionaron más de seis ejemplares por especie. El Apéndice 1 muestra la lista de ejemplares examinados.

SELECCIÓN DEL GRUPO EXTERNO

El grupo externo se seleccionó considerando taxones que presentan un gran número de sinapomorfías potenciales compartidas con el grupo interno (Nixon & Carpenter, 1993). Para ello se seleccionaron representantes de géneros de la tribu Paniceae los cuales presentan similitudes morfológicas y anatómicas con *Paspalum* (Burman, 1985; Nicora & Rúgolo de Agrasar, 1987; Watson & Dallwitz, 1989; Crins, 1991; Morrone et al., 1993) y que están relacionados filogenéticamente en análisis realizados con datos moleculares (Gómez-Martínez & Culham, 2000; Duvall et al., 2001; Giussani et al., 2001; Gómez-Martínez et al., inéd.). Dichos géneros son *Thrasya*, *Axonopus* y *Anthaenantiopsis* Mez ex Pilger.

El género *Thrasya* fue relacionado por varios autores con *Paspalum*, siendo ambos muy afines. Nicora y Rúgolo de Agrasar (1987) describen a *Thrasya* considerándola semejante al grupo Ceresia de *Paspalum* por compartir la presencia de inflorescencias con racimos espiciformes solitarios y raquis membránaceo o folioso. Por otro lado, *Thrasya* se diferencia de las especies de Ceresia por la aparente disposición uniseriada de las espiguillas y la presencia de la lemma estéril hendida. A diferencia de esto, Burman (1985) compara a *Thrasya* con los grupos Dissecta y Decumbentes del género *Paspalum* refiriendose a ciertos caracteres de *Thrasya*, como por ejemplo la lemma inferior hendida, un carácter que ha sido observado en especies del grupo Decumbentes, y la presencia de lemma inferior delgada la cual acerca a *Thrasya* al grupo Dissecta. *Thrasya* también comparte con *Paspalum* el mismo tipo anatómico y fisiológico de vía fotosintética. Giussani et al. (2001) y Duvall et al. (2001) realizaron análisis cladísticos con datos moleculares, mostrando la estrecha relación filogenética entre ambos géneros. En el presente análisis se seleccionó como representante del género *Thrasya* a *T. paspaloides* Kunth.

Watson y Dallwitz (1989) realizaron un análisis fenético en el cual muestran a *Axonopus* y *Paspalum* como géneros próximos. También Crins (1991) cita la relación fenética estrecha entre ambos. Chase (1906) y Webster (1988) muestran que dichos géneros sólo se diferencian en la orientación de la espiguilla en relación al raquis, siendo adaxial en *Axonopus* y abaxial en *Paspalum*. En relación al tipo fotosintético, *Axonopus* es fisiológicamente C_4 NADP-me y anatómicamente MS, al igual que *Paspalum*. Gómez-Martínez y Culham (2000) realizaron estudios filogenéticos con datos moleculares que confirman la cercana relación filogenética entre ambos géneros. En el presente análisis se seleccionó como representante del género *Axonopus* a *A. compressus* (Sw.) P. Beauv.

Morrone et al. (1993) realizaron la revisión del género *Anthaenantiopsis* señalando que el mismo presenta algunos caracteres morfológicos comunes con *Paspalum*. Ambos géneros presentan especies cespitosas, con inflorescencias contraídas a ligeramente abiertas, espiguillas pilosas solitarias o apareadas, antecio superior endurecido, piloso o glabro, tipo fotosintético C_4, subtipo anatómico MS y número cromosómico básico $x = 10$. Por otro lado, *Anthaenantiopsis* se diferencia de *Paspalum* por presentar inflorescencia espiciforme no unilateral; espiguillas biconvexas, gluma, flor y pálea inferior siempre presentes. Sobre la base de los caracteres anatómicos foliares descriptos por Morrone et al. (1993) se seleccionó *A. rojasiana* L. Parodi como representante del género por presentar transcorte foliar expandido al igual que la mayoría de las especies de *Paspalum* y haces vasculares con vaina parenquimática externa remanente, carácter que también se observó en *P. inaequivalve* (Aliscioni, 1999).

El reconocimiento del tipo anatómico y fisiológico asociado a la vía fotosintética constituye una serie de caracteres valiosos para realizar clasificaciones (Hattersley & Watson, 1992), especialmente dentro de la tribu Paniceae la cual incluye géneros con diferentes tipos fotosintéticos. Con la finalidad de mejorar la resolución del grupo externo e impedir incorrectas topologías del grupo interno (Nixon & Carpenter, 1993), se incluyeron como grupo externo representantes de algunos de los tipos fotosintéticos presentes en la tribu, diferentes al de *Paspalum*. De esta manera se seleccionaron *Eriochloa* Kunth (tipo fotosintético C_4 PCK, subtipo anatómico PS) y *Panicum laxum* Sw. (tipo fotosintético C_3).

A pesar de que *Eriochloa* comparte un menor número de sinapomorfías con *Paspalum*, ambos géneros presentan inflorescencias constituidas por racimos unilaterales, diferenciándose *Eriochloa* por la presencia de espiguillas con un callo basal discoide y número cromosómico básico $x = 9$ (Arriaga, 2000). Debido a que *Eriochloa* es un género monofilético y anatómicamente homogéneo (Arriaga & Aliscioni, 2000) se seleccionó *E. distachya* Kunth como representante del género.

Brown (1977) y Hattersley y Watson (1992) proponen distintos esquemas evolutivos para la tribu Paniceae, pero en ambos casos sugieren a un género anatómicamente non-Kranz como precursor de la tribu entre los que incluyen representantes C_3 de *Panicum*. Por tal motivo se asignó *Panicun la-*

xum Sw. como raíz del árbol filogenético, ya que dicha especie al igual que toda la sección *Laxa* del subgénero *Phanopyrum* es fotosintéticamente C_3 con anatomía non-Kranz (Zuloaga et al., 1992).

CARACTERES

Se identificaron un total de 36 caracteres de los cuales 14 corresponden a caracteres exomorfológicos y 22 a caracteres anatómicos foliares. De los 36 caracteres utilizados, 7 de ellos (3, 16, 21, 23, 26, 31 y 32) corresponden a caracteres multiestado los cuales han sido tratados como no aditivos. La lista de caracteres se incluye en el Apéndice 2 y la matriz básica de datos en el Apéndice 3.

Las observaciones se realizaron sobre más de 300 ejemplares de herbario pertenecientes a las siguientes instituciones: BA, BAA, BAF, CAY, COL, CPUN, CTES, FCQ, G, HUT, LPB, MEXU, MO, NY, P, PY, QCNE, SF, SI, US, USAM, USM, VEN, según siglas tomadas de Holmgren et al. (1990).

Para la obtención de los caracteres anatómicos se realizaron transcortes foliares y preparados epidérmicos los cuales fueron observados mediante la utilización de microscopia óptica. Se seleccionaron caracteres histofoliares cualitativos que resultaron ser consistentes para cada una de las especies estudiadas, evitando incorporar aquellos que pudiesen modificarse según el grado de desarrollo de la lámina. Los caracteres anatómicos fueron designados siguiendo la terminología propuesta por Ellis (1976, 1979).

También se incluyeron todos los caracteres exomorfológicos diagnósticos de los grupos informales de especies (Chase, 1929; Cialdella et al., 1995; Morrone et al., 1995, 1996; Zuloaga & Morrone, inéd.) correspondiendo principalmente a características de las inflorescencias y las espiguillas.

ANÁLISIS FILOGENÉTICO

El análisis cladístico se realizó sobre la base del principio de máxima parsimonia (Farris, 1983). Para ello se realizaron estrategias de búsqueda con pesos iguales y pesos implícitos de caracteres, utilizando los programas Nona ver. 1.8 (Goloboff, 1997a) y Pee-Wee ver. 2.8 (Goloboff, 1997b) respectivamente. Los caracteres fueron pesados de acuerdo a su grado de homoplasia, asignando menor valor a aquellos caracteres más homoplásicos (Goloboff, 1993). La relación entre el peso asignado a un carácter y su grado de homoplasia se expresa mediante una función cóncava que incluye una constante de concavidad (K) la cual puede variar según la intensidad con la que el programa penaliza a los caracteres homoplásicos. Ramírez (1998) sugiere que el valor óptimo de concavidad en un análisis, sería matriz-dependiente y plantea que la utilización de funciones moderadas de pesado ($K > 3$) encuentra patrones jerárquicos más predictivos. Goloboff (1995) considera que funciones de pesado muy intensas (valores más bajos de K) no deberían ser usadas, ya que en la práctica actúan de manera similar a un análisis de clique. En el presente análisis se discuten los resultados obtenidos con pesos iguales y con pesado implícito de caracteres bajo el valor medio de constante de concavidad ($K = 3$).

Debido al elevado número de taxones terminales se optó por el método de búsqueda heurístico empleando la opción *mult** con 100 replicaciones la cual genera árboles de Wagner con secuencias de adición al azar en cada réplica, seguido de reacomodamientos del tipo TBR, reteniéndose 20 árboles por cada réplica (*h/20*). Las búsquedas se realizaron bajo la opción *amb-* la cual colapsa las ramas que están apoyadas solamente por optimizaciones ambiguas. Las ramas de los árboles obtenidos fueron posteriormente permutadas con el comando *max**. Con el objeto de sortear posibles islas de árboles (Maddison, 1991) se utilizaron las opciones *jump*1*, *jump*2* y *jump*3* las cuales realizan reacomodamientos del tipo TBR en árboles con 1 a 3 pasos más largos respectivamente. Por último se obtuvo el árbol de consenso estricto mediante la opción nelsen (*nel*).

Como medida de apoyo para establecer el soporte de los diferentes clados se calculó el índice de Bremer (BS) (Bremer, 1994) utilizando Nona ver. 1.8 (Goloboff, 1997a) para el análisis con pesos iguales y Pee-Wee ver. 2.8 (Goloboff, 1997b) para el análisis con pesos implícitos. Asimismo, se calculó la frecuencia de grupo de Jackknife (Farris et al., 1996) utilizando el archivo de instrucciones de Nona/Pee-Wee *jak.run*, (con 1000 repeticiones, eliminando al azar el 36% de los caracteres de la matriz y utilizando la opción de búsqueda *mult*5*) y el programa *fq.exe* para calcular el árbol de consenso de mayoría (Goloboff, 1997a, b).

Para graficar los árboles y optimizar los caracteres se utilizó el programa Winclada Beta version 0.9.9 (Nixon, 1999). La optimización de caracteres fue posteriormente verificada con el comando *apo/* de los programas Nona (Goloboff, 1997a) y Pee-Wee (Goloboff, 1997b).

Resultados

El análisis cladístico realizado con pesos iguales de caracteres (matriz analizada con Nona) encontró 2903 árboles, todos ellos igualmente parsimoniosos

y de 143 pasos de longitud (Ci = 0.29, Ri = 0.69). Utilizando pesado implícito de caracteres, Pee-Wee encontró 28 árboles de 151 pasos de longitud (fit = 214.2 y fit re-escalado = 43%). A continuación se describen los resultados obtenidos del análisis con Pee-Wee, mencionando las diferencias presentes en el análisis de Nona.

Ambos análisis muestran que *Paspalum* se comporta como un grupo parafilético constituyendo un clado de alto soporte (bs = 2) junto con *Thrasya* y *Axonopus* (Fig. 1), sustentado por tres sinapomorfías: ausencia de gluma inferior (carácter que revierte secundariamente en *Thrasya*); antecio coriáceo (carácter que revierte secundariamente en *P. stellatum* y *P. polyphyllum* del grupo Ceresia [Pers.] Rchb.; *P. bertonii* y *P. lilloi* del grupo Bertoniana [sensu Chase, inéd.]; y *P. saccharoides* del grupo Saccharoidea [sensu Chase, inéd.]); y ausencia de vaina parenquimática rodeando los haces vasculares (Fig. 2A, B). Asimismo, *Anthaenontiopsis* constituye el grupo hermano de dicho clado (Fig. 1).

En el análisis realizado con Nona, el clado conformado por *Paspalum* + *Thrasya* + *Axonopus* se observa con un alto grado de colapsamiento; a diferencia de ello el árbol de consenso obtenido a partir del análisis realizado con Pee-Wee muestra una topología más resuelta. Sin embargo ambos análisis coinciden en que los únicos grupos del género *Paspalum* que constituyen clados monofiléticos son Bertoniana (sensu Chase, inéd.) con bs = 1.3, Racemosa (sensu Morrone et al., 1995) con bs = 0.5, Anachyris Chase, con bs = 5 y Filiformia (sensu Chase, 1929) con bs = 0.2; y que el grupo Bonplandiana (sensu Cialdella et al., 1995) es parafilético constituyendo un clado monofilético como grupo hermano de Racemosa (bs = 0.8). Por otro lado, los grupos Caespitosa (sensu Chase, 1929), Ceresia, Corcovadensia (sensu Chase, 1929), Eriantha (sensu Chase, inéd.), Fasciculata (sensu Chase, 1929), Linearia (sensu Chase, 1929), Livida (sensu Chase, 1929), Notata (sensu Chase, 1929), Paniculata (sensu Chase, 1929), Parviflora (sensu Chase, 1929), Plicatula (sensu Chase, 1929), Quadrifaria (sensu Barreto, 1966) y Virgata (sensu Chase, 1929) son claramente polifiléticos o constituyen politomías no resueltas. El grupo Disticha (sensu Chase, 1929) forma un clado monofilético sólo en el análisis realizado con Nona, mientras que el grupo Dilatata (sensu Chase, 1929) es monofilético sólo en el análisis de Pee-Wee; aunque en ambos casos sustentados por un bajo soporte.

A continuación se describen los grupos monofiléticos resultantes del análisis realizado con pesos implícitos (Fig. 1) y las sinapomorfías que los sustentan (Fig. 2A, B).

Paspalum lineare del grupo Linearia, junto con las especies del grupo Filiformia se unen en un clado de alto soporte (bs = 2.5) por compartir la presencia de porciones laterales del transcorte foliar inconspicuas o ausentes. *Paspalum lineare* es el taxón hermano del grupo Filiformia, siendo este último un grupo monofilético aunque de menor soporte (bs = 0.2), caracterizado por la presencia de transcorte foliar de contorno semicircular (clado 1, Fig. 1).

Paspalum proximun del grupo Linearia, es el taxón hermano del grupo Bertoniana uniéndose en un clado de bajo soporte (bs = 0.2) por compartir la presencia de parénquima incoloro en las alas del transcorte. Las especies del grupo Bertoniana forman un grupo monofilético de alto soporte (bs = 1.3) sustentado por la presencia de transcorte foliar convoluto o subconvoluto (clado 2, Fig. 1).

Paspalum orbiculatum del grupo Orbiculata, se comporta como taxón hermano del clado constituído por las especies de los grupos Plicatula, Gardneriana y Virgata sustentado con alto soporte (bs = 1.3) por compartir la presencia de antecio obovoide. Las especies de los grupos Plicatula, Gardneriana y Virgata se reúnen en un clado de alto soporte (bs = 1.8) por compartir la presencia de antecio de coloración castaño (clado 3, Fig. 1).

Todas las especies de *Paspalum* consideradas de los grupos Anachyris, Bonplandiana, Ceresia, Conjugata, Corcovadensia, Dissecta, Livida, Parviflora, Racemosa y Saccharoidea, junto con una especie de los grupos Eriantha (*P. ammodes*), Caespitosa (*P. indecorum*), Notata (*P. pumilum*) y Quadrifaria (*P. coryphaeum*), forman un clado en el cual se incluyen *Thrasya paspaloides* y *Axonopus compressus* (bs = 0.2). Dentro de este gran clado puede destacarse el nodo que reúne a las especies de Racemosa y Bonplandiana (bs = 0.8), sustentado por la presencia de células distintivas Kranz, unido a *P. repens* del grupo Dissecta como taxón hermano (bs = 0.4) (clado 4, Fig. 1). Las especies *P. malacophyllum* y *P. simplex* del grupo Anachyris se reunen por la ausencia de la gluma superior en un clado de alto soporte (bs = 5) (clado 5, Fig. 1).

Los restantes nodos del árbol de consenso, a pesar que algunos de ellos se muestran resueltos, no poseen sinapomorfías que los sustenten como clados monofiléticos.

En relación al peso que recibieron los caracteres en función de la homoplasia, los caracteres exomorfológicos: #11 (nervios de la lemma superior), 13 (forma del antecio), 14 (coloración del antecio), y anatómicos: #15 (porciones laterales del transcorte foliar), 24 (cloroplastos en la vaina mestomática), 26 (vaina parenquimática), 27 (células dis-

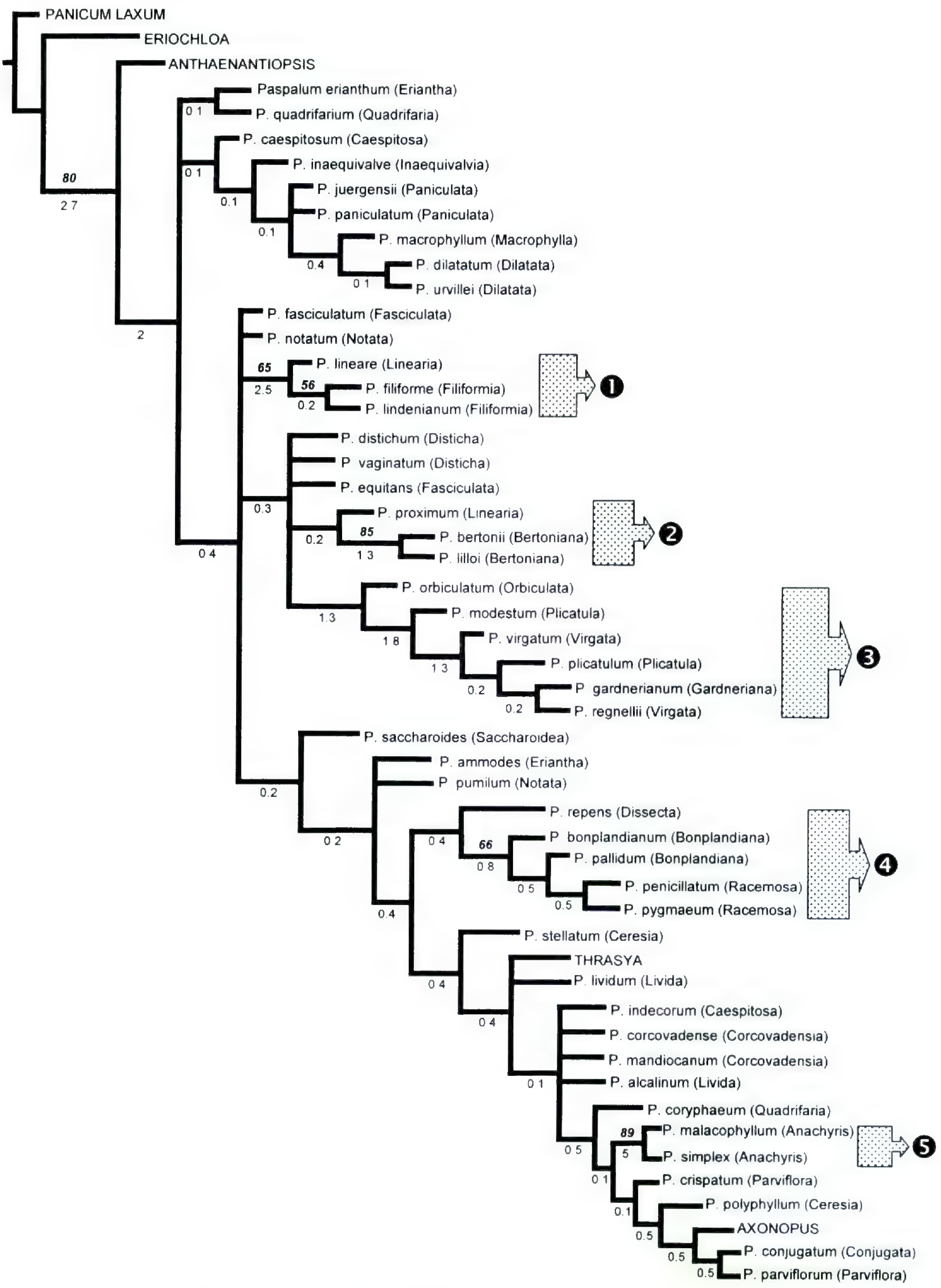

Figura 1. Árbol de consenso estricto obtenido a partir del análisis realizado con Pee-Wee (con pesado implícito de caracteres). El número sobre las ramas indica el valor de frecuencia de grupo de jackknife y el número ubicado debajo de las ramas indica el índice de Bremer. Los clados señalados (1–5) se discuten en el texto. Clado 1: *P. lineare* (Linearia) + grupo Filiformia. Clado 2: *P. proximum* (Linearia) + grupo Bertoniana. Clado 3: *P. orbiculatum* (Orbiculata) + grupo Plicatula + grupo Gardneriana + grupo Virgata. Clado 4: *P. repens* (Dissecta) + grupo Racemosa + grupo Bonplandiana. Clado 5: grupo Anachyris.

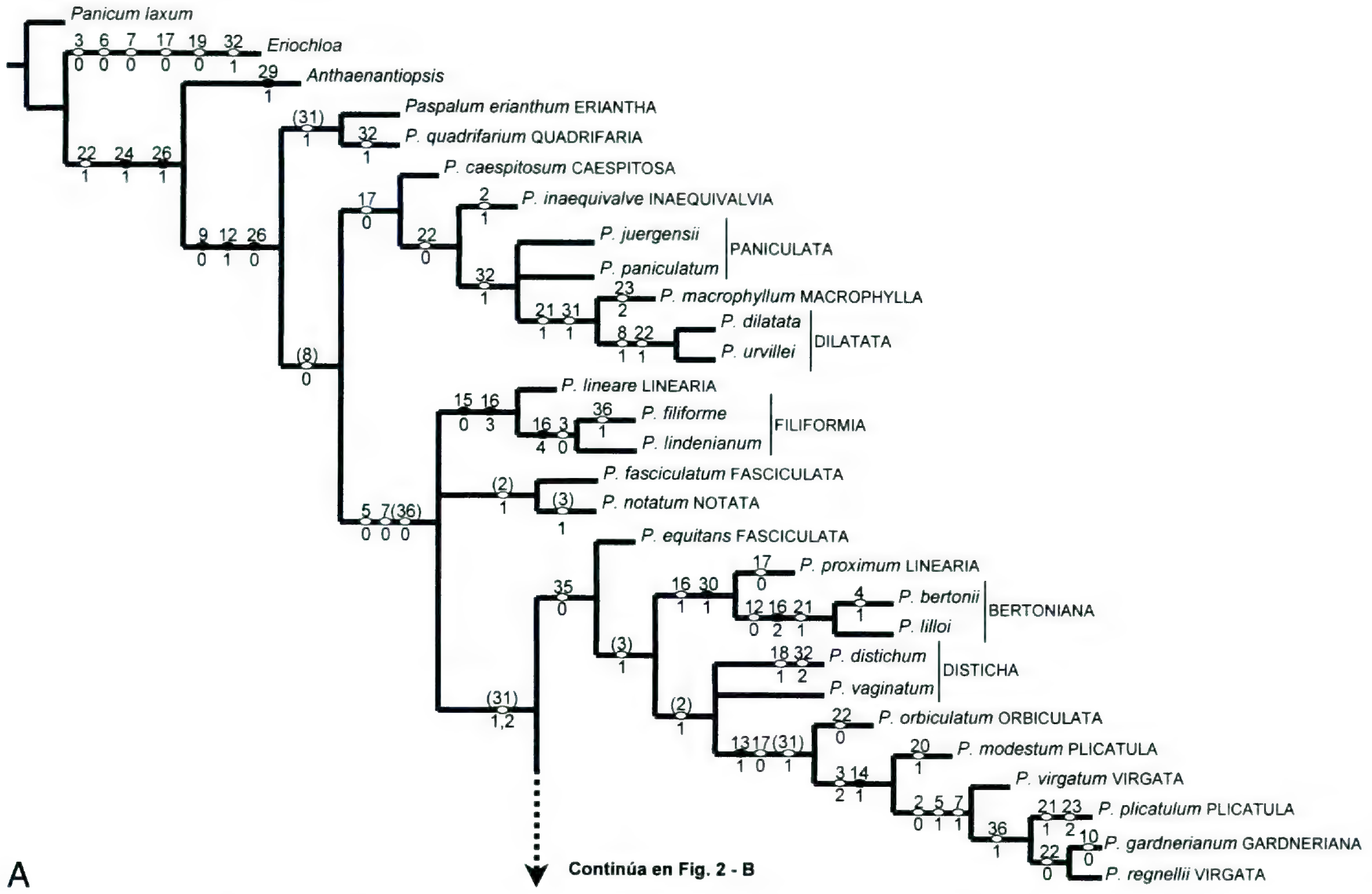

Figura 2. A, B. Optimización de los caracteres a lo largo de uno de los 28 árboles más parsimoniosos obtenidos con Pee-Wee. El número sobre las ramas indica el carácter y el número debajo de las ramas indica el estado; caracteres que no están encerrados entre paréntesis ocurren en todos los árboles y caracteres encerrados entre paréntesis ocurren sólo en el árbol que se muestra en la figura. Las sinapomorfías se indican con círculos negros y los caracteres homoplásicos se indican con círculos blancos.

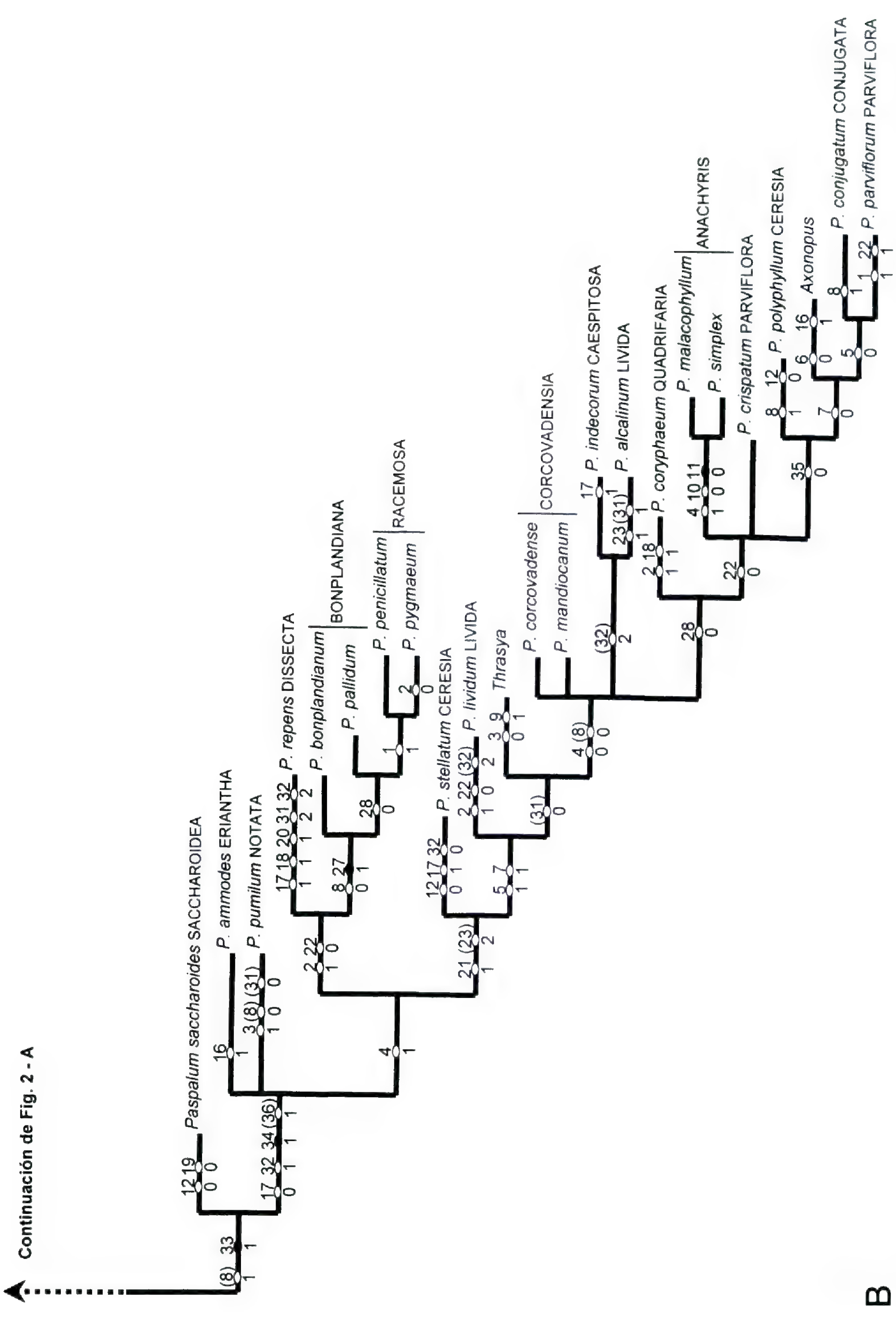

Figura 2. Continuación.

tintivas Kranz), 30 (parénquima incoloro dispuesto en las alas), 33 (macropelos adaxiales) y 34 (macropelos abaxiales) presentan peso = 10 (fit = 1), correspondiendo todos ellos a caracteres libres de homoplasia. Por otro lado, los caracteres exomorfológicos: #1 (ciclo de la planta), 6 (espiguilla abaxial), 9 (gluma inferior), 10 (gluma superior), y anatómicos: #20 (cavidades aeríferas) y 28 (células buliformes) presentan peso = 7.5 (fit = 0.75). Por último, el carácter anatómico: #18 (superficie foliar abaxial con costillas y surcos diferenciados) presenta peso = 6.0 (fit = 0.6), mientras que los restantes caracteres presentan peso ≤ 5.0 (fit ≤ 0.5).

Discusión y Conclusiones

Sobre la base de los caracteres utilizados en el presente análisis, no pudo establecerse un origen monofilético para el género *Paspalum*. Siguiendo el método práctico propuesto por Farris (1974, 1991) para identificar clados polifiléticos o parafiléticos sobre un árbol determinado, *Paspalum* se comporta en este análisis como grupo parafilético.

Los resultados obtenidos concuerdan en parte con otros estudios llevados a cabo por diversos autores, realizados sobre la base de caracteres morfológicos y moleculares, coincidiendo todos ellos en interpretar a *Paspalum* como género no monofilético (Zuloaga et al., 2000; Duvall et al., 2001; Giussani et al., 2001; Gómez-Martínez et al., inéd.).

En un estudio amplio sobre la filogenia de la tribu Paniceae realizado con datos morfológicos, Zuloaga et al. (2000) incluyeron representantes de diferentes grupos de *Paspalum*, los cuales no formaron un grupo monofilético por reunirse en una politomía no resuelta junto con géneros afines. Por otro lado, Gómez-Martínez y Culham (2000) analizaron filogenéticamente la tribu Paniceae sobre la base de datos moleculares obtenidos a partir de la secuenciación del gen de cloroplasto *trn*L-*trn*F, donde *Paspalum* es monofilético formando un clado cuyo grupo hermano es *Panicum obtusum*; sin embargo no se consideró a *Thrasya* en este estudio y la relación con *Axonopus* no queda resuelta. Posteriormente, Gómez-Martínez et al. (inéd.) sugieren la condición parafilética de *Paspalum* por incluirse en un clado sin resolución interna junto con *Anthaenantiopsis* y *Panicum obtusum*.

Recientes estudios filogenéticos sobre la subfamilia Panicoideae, aportan mayor información sobre la historia evolutiva de *Paspalum*. Giussani et al. (2001) realizaron un estudio sobre una matriz molecular obtenida a partir de la secuenciación del gen de cloroplasto *ndh*F. Estos autores incluyeron varias especies de *Paspalum* concluyendo que el mismo representa un grupo parafilético, con la incorporación dentro del mismo de *Thrasya* formando entre ambos un clado monofilético de alto soporte. Asimismo, Duvall et al. (2001) comprueban lo mismo a partir de análisis realizados con el gen de cloroplasto rpoC2.

A diferencia de los estudios mencionados anteriormente, Renvoize (1972) sugirió que *Paspalum* sería polifilético por presentar caracteres exomorfológicos semejantes en especies de grupos que están sistemáticamente distanciados dentro del género, aunque no probó su hipótesis realizando estudios de filogenia.

Los resultados obtenidos en el presente estudio muestran que solamente los grupos Anachyris, Bertoniana, Filiformia y Racemosa se resolvieron en clados con relativo soporte indicando que los mismos representarían asociaciones monofiléticas de especies.

En relación a los datos utilizados, se detectaron caracteres exomórfológicos y anatómicos libres de homoplasia los cuales proveen evidencia para la caracterización de los grupos. Dentro de los caracteres anatómicos, el desarrollo de las porciones laterales de la lámina, la presencia de células distintivas Kranz, la presencia de parénquima incoloro en las alas de la lámina y la presencia de macropelos en ambas epidermis, podrían ser valiosos en futuros estudios sistemáticos del género; algunos de ellos junto con otros caracteres exomorfológicos, definen grupos monofiléticos como el caso del clado que reune a los grupos Bonplandiana y Racemosa, en relación a las células distintivas Kranz. Dentro de los caracteres exomorfológicos utilizados tradicionalmente en la caracterización de los grupos de especies, solamente la presencia de nervios conspicuos en la lemma superior, la forma y coloración del antecio se manifestaron libres de homoplasia. Contrariamente, otros caracteres exomorfológicos como por ejemplo el hábito de la planta, el número de racimos por inflorescencia, el contorno del raquis de los racimos, la pilosidad de la espiguilla entre otros, manifestaron un alto grado de homoplasia lo cual disminuye su valor informativo debiendo ser utilizados con cierta cautela en la delimitación taxonómica de los grupos.

Según Farris (1991) solamente los grupos monofiléticos tienen una existencia real por poseer una historia evolutiva independiente; por tal motivo los resultados obtenidos no sustentan la existencia de *Paspalum* como grupo natural. Debido a la amplitud y a la diversidad observada dentro de este género, el presente estudio muestra una aproximación hacia su historia filogenética y suma una nueva evidencia a que el mismo debe ser reestruc-

turado taxonómicamente, incluyendo a *Thrasya* y *Axonopus*, aunque la inclusión de éste último no es consensuada por estudios de otra naturaleza.

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Índice de Nombres Científicos

grupo interno

Paspalum alcalinum Mez (LIVIDA)
P. ammodes Trin. (ERIANTHA)
P. bertonii Hack. (BERTONIANA)
P. bonplandianum Humb. & Bonpl. ex Flüggé (BONPLANDIANA)
P. caespitosum Flüggé (CAESPITOSA)
P. conjugatum Berg. (CONJUGATA)
P. corcovadense Raddi (CORCOVADENSIA)
P. coryphaeum Trin. (QUADRIFARIA)
P. crispatum Hack. (PARVIFLORA)
P. dilatatum Poir. (DILATATA)
P. distichum L. (DISTICHA)
P. equitans Mez (FASCICULATA)
P. erianthum Nees ex Trin. (ERIANTHA)
P. fasciculatum Willd. ex Flüggé (FASCICULATA)
P. filiforme Sw. (FILIFORMIA)
P. gardnerianum Nees (GARDNERIANA)
P. inaequivalve Raddi (INAEQUIVALVIA)
P. indecorum Mez (CAESPITOSA)
P. juergensii Hack. (PANICULATA)
P. lilloi Hack. (BERTONIANA)
P. lindenianum A. Rich. (FILIFORMIA)
P. lineare Trin. (LINEARIA)

P. lividum Trin. ex Schldl. (LIVIDA)
P. macrophyllum Kunth (MACROPHYLLA)
P. malacophyllum Trin. (ANACHYRIS)
P. mandiocanum Trin. (CORCOVADENSIA)
P. modestum Mez (PLICATULA)
P. notatum Flüggé (NOTATA)
P. orbiculatum Poir. (ORBICULATA)
P. pallidum Kunth (BONPLANDIANA)
P. paniculatum L. (PANICULATA)
P. parviflorum Rhodé ex Flüggé (PARVIFLORA)
P. penicillatum Hook. f. (RACEMOSA)
P. plicatulum Michx. (PLICATULA)
P. polyphyllum Nees ex Trin. (CERESIA)
P. proximum Mez (LINEARIA)
P. pumilum Nees (NOTATA)
P. pygmaeum Hack. (RACEMOSA)
P. quadrifarium Lam. (QUADRIFARIA)
P. regnellii Mez (VIRGATA)
P. repens Berg. (DISSECTA)
P. saccharoides Nees (SACCHAROIDEA)
P. simplex Morong ex Britton (ANACHYRIS)
P. stellatum Humb. & Bonpl. ex Flüggé (CERESIA)
P. urvillei Steud. (DILATATA)
P. vaginatum Sw. (DISTICHA)
P. virgatum L. (VIRGATA)

GRUPO EXTERNO

Anthaenantiopsis rojasiana L. Parodi
Axonopus compressus (Sw.) P. Beauv.
Eriochloa distachya Kunth
Panicum laxum Sw.
Thrasya paspaloides Kunth

APÉNDICE 1. MATERIALES EXAMINADOS.

ESPECIES DEL GRUPO INTERNO

Paspalum *subg.* Anachyris *Chase*

1. *Paspalum malacophyllum* Trin.
ARGENTINA. **Catamarca:** Altivalle de las Granadillas, *Lorentz 533* (US). PARAGUAY. **Central:** Asunción, *Rojas 6732* (US).
2. *Paspalum simplex* Morong ex Britton
PARAGUAY. **Central:** Asunción, *Hartley & Rojas 54185* (US); Trinidad, *Pavetti & Rojas 7895* (US), *Rojas 10811* (US). **Cordillera:** Piribebuy, *Rojas 13445* (US). **Chaco:** Bahía Negra, *Rojas 13813* (US). **Ñeembucú:** Estancia "Yacaré Pilar," *Rosengurtt B-5527* (US); Río Pilcomayo, *Morong 1583* (US).

Grupo Bertoniana (sensu Chase, inéd.)

1. *Paspalum bertonii* Hack.
ARGENTINA. **Misiones:** Candelaria, en isla del Río Paraná, *Montes 988* (SI); Iguazú, Salto Uruguay, *Hunziker 9941* (SI); Montecarlo, *Porta 55* (SI); San Ignacio, *Cabrera et al. 28787* (SI), *Boelcke et al. 5393* (SI); Jardín América, *Quarín 3448* (SI). BRASIL. **Paraná:** Guairá, *Reitz & Klein 12139* (US).
2. *Paspalum lilloi* Hack.
BRASIL. **Paraná:** Salto Iguassú, *Rambo 53619* (US).

Grupo Bonplandiana (sensu Cialdella et al., 1995)

1. *Paspalum bonplandianum* Humb. & Bonpl. ex Flüggé
PERÚ. **Cajamarca:** Cajamarca, *Smith & Sánchez Vega 7508* (MO, SI). **Lambayeque:** Ferreñafe, *Sagástegui et al. 12831* (HUT, SI). ECUADOR. **Carchi:** Tulcán, *Werff & Gudiño 11042* (MO, SI).
2. *Paspalum pallidum* Kunth
ECUADOR. **Imbabura:** Cotacachi, *Peñafiel & Tamayo 892* (MO, QCNE, SI). PERÚ. **Cajamarca:** Cajamarca, San Juan, *Cabanillas Soriano & Guevara 643* (CPUN, SI); Cayayup, *Ochoa 1580* (SI). **Lambayeque:** Ferreñafe, *Llatas Quiroz 1920* (HUT, SI).

Grupo Caespitosa (sensu Chase, 1929)

1. *Paspalum caespitosum* Flüggé
BELICE. **El Cayo:** Cohune Ridge, *Lundell 6426* (SI, US). MÉXICO. Las Ruinas de Coba, *Tellez & Cabrera 2353a* (MEXU, SI).
2. *Paspalum indecorum* Mez
ARGENTINA. **Corrientes:** Santo Tomé, *Krapovickas et al. 26060* (SI). **Misiones:** Cainguás, *Zuloaga & Deginani 506* (SI); Candelaria, *Montes 1357* (SI); Santa Ana, *Montes 2334* (SI); Villa Venecia, *Renvoize 3024* (SI). PARAGUAY. **Guairá:** Iturbe, *Montes 12739* (CTES).

Paspalum *subg.* Ceresia *(Pers.) Rchb.*

1. *Paspalum polyphyllum* Nees ex Trin.
BOLIVIA. **Santa Cruz:** Sara, *Steinbach 5385* (US). BRASIL. **Mato Grosso:** Tres Lagoas, *Chase 10740* (US). **Minas Gerais:** Serra de Cipó, *Archer et al. 4995* (US). **Paraná:** Ponta Grossa, *Swallen 8772* (US). **Rio de Janeiro:** Itatiaia, *Kuhlmann s.n.* (US). **Santa Catarina:** Mafra, *Smith & Reitz 12106* (US). PARAGUAY. **Alto Paraná:** *Fiebrig 6222* (US). **Amambay:** *Rojas 10209* (US). **Central:** Ypacaraí, Lago Ypacaraí, *Hassler 11561* (US).
2. *Paspalum stellatum* Humb. & Bonpl. ex Flüggé
ARGENTINA. **Misiones:** Posadas, *Ekman 594* (US). COLOMBIA. **Magdalena:** Santa Marta, *Smith 142* (US). PARAGUAY. **Amambay:** *Hassler 11058* (US). **Caaguazú:** Estancia "Plate San José," *Rosengurtt B 5883* (US). **Central:** Asunción, *Rojas 11005* (US); Tarumandy, *Schinini 6207* (US). **Cordillera:** Cordillera de Altos, *Fiebrig 664* (US).

Grupo Conjugata (sensu Chase, 1929)

1. *Paspalum conjugatum* Berg.
ARGENTINA. **Jujuy:** Valle Grande, *Taylor et al. 11377* (MO, SI). **Misiones:** Apóstoles, *Cabrera & Saénz 29087* (SI); Candelaria, *Montes 2455* (SI); El Dorado, *Burkart 14544* (SI); Gral. Belgrano, *Hunziker et al. 11016* (SI); Iguazú, *Montes 6950* (SI); Posadas, *Burkart 14024* (SI); San Javier, *Cabrera et al. 28659* (SI). BOLIVIA. **Santa Cruz:** Sara, *Steinbach 1910* (SI); Warnes, *Zabala 627* (SI).

Grupo Corcovadensia (sensu Chase, 1929)

1. *Paspalum corcovadense* Raddi
BRASIL. **Rio de Janeiro:** Leblón, *Rosengurtt 3377* (US). **Rio Grande do Sul:** *Arth 1102* (US). **Santa Catarina:** Itajaí, *Smith & Reitz 6076* (US). **São Paulo:** Capital Chávaca dos Morrinhos, *Pickel 5803* (US).
2. *Paspalum mandiocanum* Trin.
BRASIL. **Rio de Janeiro:** Dist. Federal, *Black & Froes 51-11331* (US). PARAGUAY. **Alto Paraná:** Irala, *Montes 11029* (US). **Central:** Asunción, *Rojas 13346* (US); Lago Ypacaraí, *Hassler 12481* (US). **Guairá:** Villarrica, *Rosengurtt B-5929* (US). **Itapúa:** En-

carnación, *Rojas 11191* (US). **Paraguarí:** Caapucú, *Anderson 1151* (US); s.l., *Rojas 13346II* (US).

Grupo Dilatata (sensu Chase, 1929)

1. *Paspalum dilatatum* Poir.
ARGENTINA. **Buenos Aires:** Bañados entre San Fernando y Pacheco, *Correa s.n* (SI); La Plata, *Cabrera 3420* (SI). **San Luis:** Pedernera, *Rosa 48* (SI). **Santa Fe:** Castellanos, *Alonso 31* (SI). BRASIL. **Rio Grande do Sul:** Bagé, *Barreto 1601* (SI); São Gabriel, *Barreto 916* (SI); São Simao, *del Mato 12382* (SI). **Santa Catarina:** Agua Doce, *Smith & Klein 13529* (SI). CUBA. **Pinar del Río:** near Mariel, *Ekman s.n.* (US). URUGUAY. **Montevideo:** Atahualpa, *Herter et al. 334* (SI).
2. *Paspalum urvillei* Steud.
BRASIL. **Mato Grosso:** vicinity of Dourados, *Chase 10951* (US). **Paraná:** Coloniba, *Dombrowski 4391* (US). **Santa Catarina:** Itajaí, *Klein 2749* (US). **São Paulo:** Alto da Serra, *Lemos 31504* (US). COLOMBIA. **Antioquia:** Urrao, *Pohl & Betancur 15504* (US). PARAGUAY. **Guairá:** Villarrica, *Jorgensen 3535* (US), *Jorgensen 3635* (US).

Grupo Dissecta (sensu Morrone et al., 1996)

1. *Paspalum repens* Berg.
ARGENTINA. **Buenos Aires:** Delta del Paraná, *Burkart 4355* (SI), *Burkart 4343* (SI). **Chaco:** Río de Oro, *Holmberg s.n.* (SI). **Entre Ríos:** La Paz, *Pedersen 8322* (SI); Puerto La Paz, *Burkart et al. 26830* (SI). **Santa Fe:** Garay, *León & Fossati 922* (SI); San Jerónimo, *Morello 16873* (SI); Islas del Río Paraná, *Morello 500* (SI). PERÚ. **Loreto:** Maynas, *Gentry 42338* (MO, SI). VENEZUELA. **Guárico:** Camaguán, *Zuloaga et al. 4353* (SI, VEN).

Grupo Disticha (sensu Chase, 1929)

1. *Paspalum distichum* L.
BOLIVIA. **Cochabamba:** s.l., *Hitchcock 22793* (US). **Potosí:** sur de Chichas, *Hitchcock 22882* (US). COLOMBIA. **Chocó:** s.l., *Hitchcock 19908* (US). ECUADOR. **Pichincha:** Tumbaco, *Asplund 6571* (US). HAITÍ. Area betw. Terrier Rouge and Fort Liberté, *Bartlett 17483* (US). PARAGUAY. **Central:** in regione lacus Ypacaraí, *Hassler 12452* (US); playas del Río Paraguay, *Pavetti & Rojas 9448* (US); in regione cursus inferioris fluminis Pilcomayo, *Rojas 322* (US). PERÚ. **Piura:** Hacienda Buenos Aires, *Anderson 668* (US). PUERTO RICO. **Ponce:** s.l., *Chase 6483* (US).
2. *Paspalum vaginatum* Sw.
BRASIL. **Bahia:** Itacaré, *Belém & Peirheiro 2985* (US). **Pará:** Marapanim, *Davidse et al. 17785 B* (US). COLOMBIA. **Magdalena:** Santa Marta, *Smith 179* (US). CUBA. **Habana:** Guanimar, *León 14168* (US). GUYANA FRANCESA. **Isla de Cayena:** Anse de Montabo, *Hoff 5168* (CAY, P, US). PARAGUAY. **Paraguarí:** Caacupú, *Anderson 1125* (US). PERÚ. **La Libertad:** Trujillo, *Angulo & Ridoutt 0279* (US). **Lima:** Chorillos, *Asplund 10906* (US).

Grupo Gardneriana (sensu Chase, 1929)

1. *Paspalum gardnerianum* Nees
BRASIL. **Goiás:** Formosa, *Glaziou 22583* (P); s.l., *Glaziou 22586* (US). **Maranhão:** Barra do Corda to Grajahú, *Swallen 3652* (US). **Piauí:** s.l., *Gardner 3507* (P). GUAYANA. Ebini Experimental Station, *Harrison 1786* (US). COLOMBIA. **Arauca:** 10 km SW of Cravo Norte, *Blydnstein 1522* (US).

Grupo Eriantha (sensu Chase, inéd.)

1. *Paspalum ammodes* Trin.
BRASIL. **Goiás:** Serra do Caiapó, *Irwin & Soderstrom 7040* (SI). **Paraná:** Jaguarihyva, *Dusén 16025* (G). **São Paulo:** San Jose dos Campos, *Morello s.n.* (SI).
2. *Paspalum erianthum* Nees ex Trin.
BRASIL. **Goiás:** s.l., *Glaziou 22491* (G), *Glaziou 22489* (G), *Glaziou 22589* (G). **Paraná:** Turma 23, *Dusén 15669* (G). **Rio de Janeiro:** s.l., *Glaziou 15635* (G). PARAGUAY. **Amambay:** in regione calcarea cursus superioris fluminis Apa, *Hassler 11924* (G); Sierra de Amambay, Lomadas Esperanza, *Hassler 10765* (G).

Grupo Fasciculata (sensu Chase, 1929)

1. *Paspalum equitans* Mez
ARGENTINA. **Corrientes:** Santo Tomé, *Quarín et al. 2753* (CTES, SI, US). PARAGUAY. **Paraguarí:** Este de la Cordillera de Villa Rica-Marais, *Balansa 87* (P).
2. *Paspalum fasciculatum* Willd. ex Flüggé
BRASIL. **Pará:** Boa Vista, *Swallen 31651* (US). COLOMBIA. **Bolívar:** Magangue, *Pennell 3933* (NY, US); Island of Mompos, *Curran 366* (US). **Magdalena:** Costa del Caribe, *Dugand 5259* (COL, US). PARAGUAY. **Central:** s.l., *Morong 535* (US).

Grupo Filiformia (sensu Chase, 1929)

1. *Paspalum filiforme* Sw.
CUBA. **Pinar del Río:** Mariel, *Ekman 946* (SI, US).
2. *Paspalum lindenianum* A. Rich.
CUBA. **Pinar del Río:** Mariel, *Ekman 947* (SI, US).

Grupo Inaequivalvia (sensu Chase, inéd.)

1. *Paspalum inaequivalve* Raddi
BOLIVIA. **La Paz:** Milluguaya, Caripata, *Hitchcock 22672* (US). BRASIL. **Mato Grosso do Sul:** Corumbá on Rio Paraguay, *Chase 11133* (US). PARAGUAY. **Caacupé:** s.l., *Archer et al. 4799* (US). **Central:** in regione lacus Ypacaray, *Hassler 12401* (US); s.l., *Morong 557* (US). **Cordillera:** Caacupé, *Ramírez 406* (US); in regione cursus inferioris fluminis Pilcomayo, *Rojas 96* (US); s.l., *Balansa 106* (US).

Grupo Linearia (sensu Chase, 1929)

1. *Paspalum lineare* Trin.
BRASIL. **Ceará:** s.l., *Gardner 2979* (P). **Goiás:** Capalinha, *Glaziou 22475* (G). **Minas Gerais:** s.l., *Weddell 1839* (P). **Piauí:** s.l., *Gardner 2975* (G, P). **São Paulo:** s.l., *Löfgren 351* (P); s.l., *Riedel 949* (G); s.l., *Moricand 2975* (G).
2. *Paspalum proximum* Mez
BRASIL. **Santa Catarina:** Abelardo Luz, *Smith & Klein 13319* (P); Agua Doce, *Smith & Klein 13653* (US); Fachinal dos Guedes, *Smith & Klein 14014* (US). **Paraná:** Jaguariahyva, *Jonsson 307a* (P). **São Paulo:** Butantan, *Gehrt 28535* (US); Estacás Calmon Vianna, *Pickel 5520* (US); Itaripina, Campo Alegre, *Black 51-10994* (US). PARAGUAY. **Guairá:** Villa Rica, *Balansa 69* (G).

Grupo Livida (sensu Chase, 1929)

1. *Paspalum alcalinum* Mez
   COLOMBIA. **Cundinamarca:** La Esperanza, *García Barriga 10009* (US). PARAGUAY. **Alto Paraguay:** Puerto Casado, *Rojas 5597* (US); Cerro Galván, *Rojas 2778* (US). **Chaco:** F. C. Casado, *Rosengurtt B-5863* (US), s.l., *Rosengurtt B-5470* (US); Estancia Gustafson, *Ramírez 190* (US).
2. *Paspalum lividum* Trin. ex Schldl.
   ARGENTINA. **Entre Ríos:** Paraná, *Zucol 661* (SI); San José, Colón, *Zucol 655* (SI). **Santa Fe:** 9 de Julio, *Pensiero & Vegetti 2740* (SF); San Justo, *Pensiero 2736* (SF).

Grupo Macrophylla (sensu Chase, inéd.)

1. *Paspalum macrophyllum* Kunth
   COLOMBIA. **Antioquia:** Fredania, *Archer 505* (US); Cocarina, *Lindig 14* (P). **Cauca:** La Manuelita, *Pittier 897* (US).

Grupo Notata (sensu Chase, 1929)

1. *Paspalum notatum* Flüggé
   COLOMBIA. **Antioquia:** Medellín, *Archer 783* (US). **Cauca:** La Manuelita, *Pittier 845* (US). **Cundinamarca:** Fusagasuga, *Juzepczuk 5317* (US). **El Valle:** Hacienda "El Trejo," *Hernando García 6412* (US). **Huila:** Algeciras, *Fosberg 19240* (US); s.l., *Dawe 854* (US). PARAGUAY. **Central:** Jardín Botánico, *Archer 4721* (US); San Bernardino, *Rojas 1006* (US). **Ñeembucú:** Estancia del Sr. Medina Pilar, *Ramírez 131* (US). **Paraguarí:** betw. Piribebuy and Paraguarí, *Jorgensen 3537* (US); *Rojas 110* (US).
2. *Paspalum pumilum* Nees
   BRASIL. **Rio de Janeiro:** s.l., *Sellow s.n.* (P); Copacabana, *Glaziou 4343* (P); Jardín Botanico Alta Boa Vista, *Chase 8443* (US). **Santa Catarina:** Blumenau, *Klein 10366* (US); Florianopolis, Canasvieiras, *Klein et al. 6478* (US).

Grupo Orbiculata (sensu Chase, 1929)

1. *Paspalum orbiculatum* Poir.
   BOLIVIA. **Pando:** Madre de Dios, *Nee 31353* (US). COLOMBIA. **Amazonas:** Trapecio amazónico, *Schultes & Black 8508* (US); Boca Loreto–Yaco, *Schultes & Black 46-171* (US). **Antioquia:** alrededores del Río Ampurrumiadó, *Gutiérrez & Barkley 17C178* (US). **El Valle:** Río Calema, *Cuatrecasas 21118* (US). PARAGUAY. **Central:** Carapeguá, *Rojas 3350* (US); Arroyo Tobaty, *Archer 4839* (US).

Grupo Paniculata (sensu Chase, 1929)

1. *Paspalum juergensii* Hack.
   BOLIVIA. **La Paz:** Nor Yungas, *Beck 9152* (US); Sur Yungas, *Hitchcock 22627* (US). BRASIL. **Paraná:** Serra do Mar, *Dusèn 3624* (SI). **Rio Grande do Sul:** Brasilia, *Rambo 41248* (US); Inst. Agr. Sul-Pelotas- R. G- Sul. Mato (Hôrto Botânico), *da Costa Sacco 119* (US). COLOMBIA. **Putumayo:** Paianza el Fabaño, *Gamía 4526* (US). ECUADOR. **Tungurahua:** Valley of Pastaza River, *Hitchcock 21842* (US), *Hitchcock 21749* (US).
2. *Paspalum paniculatum* L.
   BRASIL. **Bahia:** Rua Federacão, *Chase 7868* (US). COLOMBIA. **Boyacá:** Valley of Rio Pomera, (US 2206414). **Cauca:** El Tambo, *Godfrey s.n.* (US). **Cundinamarca:** Estación Santana, *Dugand & Jaramillo 3891* (US). **El Valle:** Cordillera Occidental, *Cuatrecasas 19685* (US). ECUADOR. **Imbabura:** Lita, *Acosta-Solís 12567* (US). PARAGUAY. **Amambay:** in altiplanitie et declivibus "Sierra de Amambay," *Rojas 10134* (US), *Rojas 10738* (US). **Caazapá:** Abai region San Juan Nepomuceno, *Rojas 5835* (US). TRINIDAD TOBAGO. **Port of Spain:** s.l., *Hitchcock 10036* (US).

Grupo Parviflora (sensu Chase, 1929)

1. *Paspalum crispatum* Hack.
   BRASIL. **Mato Grosso:** Santa Rita do Araguaya, *Chase 11844* (US), *Chase 12051* (US). PARAGUAY. **Amambay:** in altiplanitie Sierra de Amambay, *Hassler 11975* (US).
2. *Paspalum parviflorum* Rhodé ex Flüggé
   BRASIL. **Amapá:** Rio Pedreira, *Pires & Cavalcante 52142* (US); Macapá, *Black & Fróes 51-12300* (US); betw. Rios Cuyubin and Flechal, *Pires & Cavalcante 52379* (US). **Mato Grosso:** entre Barão de Melgaco e Pimienta Buena, *Kuhlmann 1682* (US); Fazenda Patizal, *Richards 6489* (US). **Pará:** Marajo Island, *Goeldi 95* (US); Pombal, Paraná do Tapará, *Black 52-15565* (US); s.l., *Capanema 5416* (US). GUYANA FRANCESA. Route de Simamory Leándre, *Hoock 1136* (US); s.l., *Le Prieur 66* (US).

Grupo Plicatula (sensu Chase, 1929)

1. *Paspalum modestum* Mez
   ARGENTINA. **Corrientes:** Capital, *Ahumada 608* (CTES, SI); Itatí, Arrocera Rzepecki, *Ahumada et al. 920* (CTES, SI); Solari, Curuzú Cuatiá, *Vander Shuijs 1393* (SI). **Entre Ríos:** La Paz, *Burkart & Bacigalupo 21084* (SI); Puerto Soto, *Burkart & Bacigalupo 21093* (SI). PARAGUAY. **Central:** orillas de lago Ypacaraí, *Hicken 111* (SI); San Bernardino, *Rojas 1111* (US).
2. *Paspalum plicatulum* Michx.
   BRASIL. **Paraná:** Curityba, *Dusén 13491* (G). **Rio Grande do Sul:** Bagé, Estancia Taruma, *Barreto 1600* (SI); Faz. Experimental de Criaçao Cinco Cruzes, *Barreto 1377* (SI); Potrero N° 24, *Barreto 1475* (SI); 12 km de Vacaría, *Quarín 1720* (CTES, SI); Passo Fundo, *Quarín 1718* (CTES, SI). **Santa Catarina:** Agua Doce, *Smith & Klein 13546* (SI).

Grupo Quadrifaria (sensu Barreto, 1966)

1. *Paspalum coryphaeum* Trin.
   BRASIL. **Bahia:** subida al pico das Almas, *Zuloaga et al. 4837* (SI); Br-242, *Zuloaga et al. 4774* (SI). **Minas Gerais:** Morro da Gloria, *Glaziou 18684* (P). **Rio de Janeiro:** Nova Friburgo, *Glaziou 13328* (P); Pão de Assucar, *Chase 8393 III* (US).
2. *Paspalum quadrifarium* Lam.
   ARGENTINA. **Corrientes:** Curuzú-Cuatiá, *Nicora 4644* (SI). URUGUAY. **Artigas:** Arroyo Guavieyú, *Rosengurtt 11328* (US); Flores, Río Yí, *Rosengurtt 641* (US).

Grupo Racemosa (sensu Morrone et al., 1995)

1. *Paspalum penicillatum* Hook. f.
   BOLIVIA. **La Paz:** Nor Yungas, *Beck 9158* (SI, UMSA); 0.7 km W of Chuspipata, *Solomon 13692* (MO, SI). PERÚ. **La Libertad:** Otuzco, *Sagástegui et al. 11569* (HUT, SI). **Lima:** Chancay, *Trovar 375* (SI,

USM); Lima, Lomas de Atocongo, *Cerrate 832* (SI, USM).

2. *Paspalum pygmaeum* Hack.
   ARGENTINA. **Jujuy:** Santa Ana, *Burkart & Troncoso 11670* (SI); s.l., *Parodi 16452* (SI). **Tucumán:** Tafí, *Burkart 5280* (SI). BOLIVIA. **Cochabamba:** Quillacollo, *Beck et al. 18079* (LPB, SI). **La Paz:** Ingavi, *Villavicencio 288* (LPB, SI); Murillo, 17 km al este de La Cumbre por el camino Unduavi, *Solomon 18263* (LPB, MO, SI); Omasuyos, Tiquina, *Beck 2923* (SI). PERÚ. **Ancash:** Bolognesi, *Cerrate 1375* (SI, USM). **Huancavelica:** Huancavelica, Patacancha, *Tovar 3155* (SI, USM). **Junín:** Huancayo, *Tovar 2164* (USM).

Grupo Saccharoidea (sensu Chase, inéd.)

1. *Paspalum saccharoides* Nees
   BOLIVIA. **La Paz:** Quebrada de Zongo, *Zuloaga & Vázquez Ávila 1831* (SI). COLOMBIA. **Meta:** 10 km de la carretera Villavicencio a Bogotá, *Zuloaga 3955* (SI); Quindio, Montenegro, *Zuloaga & Londoño 4186* (SI). PANAMÁ. **Cocle:** savannas near El Valle, *Duke & Mussell 6612* (SI, US). **Chiriquí:** Fotuna Dam area, *Churchill & Churchill 6141* (MO, SI). VENEZUELA. **Bolívar:** entre Piedra de la Virgen y la parte alta de la Escalera, *Zuloaga et al. 4394* (SI, VEN). **Distrito Federal:** entre Caracas y La Guaira, *Burkart 16994 a* (SI).

Grupo Virgata (sensu Chase, 1929)

1. *Paspalum regnellii* Mez
   ARGENTINA. **Misiones:** Iguazú, *Guaglianone et al. 995* (SI). BRASIL. **Minas Gerais:** Viçosa, *Chase 9428* (SI). **Rio de Janeiro:** Petrópolis, *Glaziou 9049* (P). PARAGUAY. **Central:** Asunción, *Rojas 5800* (SI).
2. *Paspalum virgatum* L.
   GUYANA. **Georgetown:** along Lamaha Canal, *Hitchcock 16552* (US). JAMAICA. Savana entre Ewarton y Linstead, *Hitchcock 576* (P). TRINIDAD Y TOBAGO. **Tobago:** Frunchfield, *Eggers 5553* (P). MÉXICO. **Tabasco:** Tenosique, *Matuda 3519* (MEXU).

ESPECIES DEL GRUPO EXTERNO

Anthaenantiopsis rojasiana L. Parodi
   ARGENTINA. **Corrientes:** Santo Tomé, *Burkart 19628* (BAA, SI); Estancia Garruchos, *Cabrera 11871* (BAA). **Misiones:** Posadas, *Parodi 4552* (BAA).

Axonopus compressus (Sw.) P. Beauv.
   ARGENTINA. **Santa Fe:** Arroyo Natulipiahué, *Castellanos 19443* (BA). BOLIVIA. **Santa Cruz:** Sara, *Steinbach 1865* (BA), *Steinbach 6990* (BA). PARAGUAY. **Alto Paraná:** Puerto Bertoni, *Bertoni 11313* (BA). URUGUAY. s.l., *Hauman 11212* (BA).

Thrasya paspaloides Kunth
   BRASIL. **Distrito Federal:** Brasilia, *Zuloaga s.n.* (SI).

Eriochloa distachya Kunth
   BOLIVIA. **Santa Cruz:** Velasco, *Rua & Carrión 450* (BAA); Sara, Cauce viejo del Río Dolores, *Steinbach 1940* (BA). PARAGUAY. **Amambay:** in regione calcarea cursus superioris fluminis Apa, *Hassler11034* (BAA, BAF, G).

Panicum laxum Sw.
   ARGENTINA. **Buenos Aires:** Isla Martín García, *Parodi 46626* (BAA). **Chaco:** Puerto Antequera, *Zuloaga et al. 3319* (SI). **Corrientes:** 42 km E de Ituzaingó, *Zuloaga et al. 2298* (SI).

APÉNDICE 2. LISTA DE CARACTERES.

CARACTERES EXOMORFOLÓGICOS

1. Ciclo de vida de la planta: (0) perenne; (1) anual.

La mayoría de las especies del género son perennes; a pesar de ello existen especies anuales las cuales pertenecen a diferentes grupos. Ejemplo de esto son las especies del grupo Racemosa (Morrone et al., 1995), como así también algunas especies de los grupos Parviflora y Plicatula (Chase, 1929). Según Rua y Weberling (1995) las especies anuales ocupan hábitats específicos como altas montañas, márgenes de bosques montañosos o sabanas con una marcada estación seca. Por otro lado, Morrone et al. (1995) interpretan al ciclo de vida anual como un carácter evolucionado dentro del género, basándose en los criterios evolutivos propuestos por Stebbins (1982), Watson y Dallwitz (1982) y Davidse (1987).

2. Hábito de la planta: (0) cespitosa; (1) no cespitosa.

Rua y Weberling (1995) desarrollaron distintos modelos para describir las formas de crecimiento presentes en *Paspalum*; considerando que el hábito cespitoso es el más frecuente en el género. Por otro lado, las especies no cespitosas pueden presentar tallos decumbentes, rastreros, largamente rizomatosos o estoloníferos; pertenecen a grupos restringidos dentro del género los cuales desarrollan bajo condiciones ambientales particulares.

3. Número de racimos en las inflorescencias: (0) 1 racimo; (1) 2 racimos; (2) más de 2 racimos.

La inflorescencia de *Paspalum* ha sido descripta tradicionalmente como una panoja constituida por racimos espiciformes insertos a lo largo de un eje. Vegetti (1987) describe a la inflorescencia de *Paspalum* como de tipo politélico debido a que los racimos o paracladios largos terminan en una espiguilla estéril o en una porción estéril del raquis. Según Vegetti (1987) y Rua y Weberling (1995) las diferencias estructurales de las inflorescencias dentro de *Paspalum* se deben a un desarrollo variable de la zona paracladial con un truncamiento del eje principal, seguido de un proceso de reducción en el número de paracladios y en el crecimiento de la zona internodal del eje principal de la inflorescencia. Basado en estos conceptos, Vegetti (1987) considera que las inflorescencias con 1 ó 2 racimos serían más evolucionadas dentro del género.

4. Contorno del raquis de los racimos de las inflorescencias: (0) subtrígono; (1) expandido.

El raquis de los racimos presenta un transcorte subtrígono en la mayoría de las especies de *Paspalum*, con una carina en la cara dorsal disponiéndose las espiguillas hacia ambos lados de la misma generando racimos espiciformes. En algunas especies de *Paspalum*, el raquis de los racimos se presenta anchamente expandido, con proyecciones laterales hialinas o foliosas. Esto se observa en las especies de los grupos Ceresia, Dissecta, Racemosa y Bonplandiana, como así también en algunas especies de los grupos Lachnea, Gardneriana y Plicatula. *Thrasya* también comparte con las especies anteriormente citadas la presencia de inflorescencias con raquis expandido.

5. Espiguilla adaxial: (0) ausente; (1) presente.

Las espiguillas que se disponen solitarias sobre el raquis se definen con posición adaxial cuando el dorso de

la gluma inferior se orienta contra el raquis del racimo. Pero es muy frecuente observar dentro de la tribu Paniceae la presencia de espiguillas pareadas; en dicho caso Zuloaga et al. (2000) consideran que la espiguilla adaxial es homóloga a la espiguilla de posición terminal que corresponde a una ramificación secundaria del raquis del racimo.

6. *Espiguilla abaxial: (0) ausente; (1) presente.*

Las espiguillas que se disponen solitarias sobre el raquis se definen con posición abaxial cuando el dorso de la gluma inferior se orienta opuesto al raquis del racimo. Según Zuloaga et al. (2000), en las especies de la tribu Paniceae que presentan espiguillas pareadas, la espiguilla abaxial es homóloga a la espiguilla de posición axial, la cual se genera a partir de una ramificación terciaria del raquis del racimo.

7. *Número de hileras de espiguillas por racimo: (0) dos; (1) cuatro.*

Los racimos presentan dos hileras de espiguillas cuando las espiguillas son solitarias y cortamente pediceladas. En este caso, es simple determinar la orientación de la misma (Clayton & Renvoize, 1986), siendo adaxial en *Axonopus* y abaxial en las especies de *Paspalum* con espiguillas solitarias. Sin embargo, dentro del género *Paspalum* algunas especies poseen espiguillas pareadas, observándose cuatro hileras de espiguillas por racimo. El número de hileras de espiguillas en cada racimo o paracladio largo es una consecuencia del grado de ramificación del eje de los paracladios cortos (Rua & Weberling, 1995). La presencia de espiguillas dispuestas en pares es un carácter frecuente dentro de las Paniceae y se considera que es una condición primitiva siendo interpretada como una sinapomorfía potencial de la tribu (Kellogg, 2000).

8. *Pilosidad de la espiguilla: (0) glabra; (1) pilosa.*

La presencia de espiguillas provistas de pelos es probablemente una especialización para la dispersión por adhesión o a través del viento de la diáspora. Ejemplos de esto son *Paspalum conjugatum* el cual presenta espiguillas con pelos distribuidos sobre los márgenes formando un delicado borde piloso, altamente efectivo para la dispersión por adhesión; y *P. saccharoides* que crece en zonas algo elevadas y presenta espiguillas con largos pelos sedosos intercalados con pelos más cortos los cuales facilitan la dipersión mediante el viento (Davidse, 1987). El grupo Ceresia se caracteriza por la presencia de espiguillas conspicuamente pilosas, con pelos sedosos distribuidos más densamente sobre los márgenes; un patrón similar se observa en especies de los grupos Eriantha y Bertoniana (Zuloaga & Morrone, inéd.). En otros grupos de *Paspalum*, como Dilatata y Dissecta, la presencia de espiguillas pilosas es un carácter polimórfo dentro del grupo.

9. *Gluma inferior: (0) ausente; (1) presente.*

Una de las características importantes a nivel genérico en *Paspalum* es la supresión de gluma inferior en las espiguillas, carácter también presente en *Axonopus*. Sin embargo, muchas especies de *Paspalum* pueden presentar alguna espiguilla del racimo con la gluma inferior parcialmente desarrollada, como ocurre en algunos ejemplares de *P. distichum* y *P. vaginatum* (Chase, 1929).

10. *Gluma superior: (0) ausente; (1) presente.*

La ausencia de gluma superior es un carácter poco frecuente dentro de *Paspalum*, siendo una característica distintiva del subgénero *Anachyris*. A pesar de ello, algunas especies de dicho subgénero poseen gluma superior con diferentes grados de desarrollo (Morrone et al., 2000). Asimismo, algunas especies pertenecientes a los grupos Racemosa, Gardneriana, Parviflora y Reimaria, también carecen de gluma superior (Zuloaga & Morrone, inéd.). Renvoize (1972) considera que la reducción de la gluma superior se pudo haber originado independientemente varias veces dentro del género, posiblemente como una tendencia adaptativa.

11. *Nervios de la lemma superior: (0) conspicuos; (1) no conspicuos.*

La presencia de lemma superior con nervios conspicuamente marcados es característica del subgénero *Anachyris*; la misma presenta la cara abaxial surcada por cinco nervios prominentes, siendo ésta una sinapomorfía del subgénero (Morrone et al., 2000).

12. *Consistencia del antecio: (0) membranáceo; (1) coriáceo.*

Según Cialdella y Vega (1996) el endurecimiento y especialización del antecio superior en las Paniceae podría interpretarse como una consecuencia de la reducción en el número de brácteas que conforman la espiguilla. Davidse (1987) interpreta que muchas especies de *Paspalum*, juntamente con otros géneros de la misma tribu presentan antecios de consistencia más dura debido a que estarían adaptados a mecanismos de dispersión de la diáspora a través de animales herbívoros. La dureza del antecio permitiría que el mismo se mantenga viable aún después de atravesar el tracto digestivo del animal.

13. *Forma del antecio: (0) elipsoide; (1) obovoide.*
14. *Coloración del antecio: (0) pajizo; (1) castaño.*

CARACTERES ANATÓMICOS FOLIARES

15. *Porciones laterales del transcorte: (0) ausentes o inconspicuas; (1) desarrolladas.*

La mayoría de las especies de *Paspalum* presentan hojas planas o expandidas; sin embargo en algunos casos las alas laterales de la lámina no desarrollan, originando hojas de aspecto filiforme las cuales presentan transcortes foliares reducidos a la zona de la costilla central de la lámina (Aliscioni, 2000).

16. *Contorno del transcorte foliar: (0) expandido o en forma de "V" abierta; (1) conduplicado; (2) convoluto a subconvoluto; (3) elíptico; (4) semicircular* (ver Aliscioni, 2000, fig. 3).
17. *Superficie foliar adaxial con costillas y surcos diferenciados: (0) ausente; (1) presente.*
18. *Superficie foliar abaxial con costillas y surcos diferenciados: (0) ausente; (1) presente.*
19. *Costilla central: (0) indiferenciada; (1) diferenciada.*
20. *Cavidades aeríferas: (0) ausentes; (1) presentes.*

Las cavidades aeríferas observadas en distintas especies de *Paspalum* se presentan en la costilla central de la lámina; las mismas pueden presentar distinto grado de desarrollo pero en todos los casos se originan a partir de la lisis de células parenquimáticas incoloras. La presencia de dicho carácter se asocia a especies que habitan lugares con exceso de humedad (Aliscioni, 2000, fig. 2).

21. *Diferenciación y alternancia de haces vasculares: (0) un haz de 3° orden entre un haz de 1° y uno de 2°*

orden; (1) tres haces de 3° orden entre un haz de 1° y uno de 2° orden; (2) sin distinción entre haces de 2° y 3° orden.

22. *Posición de los haces vasculares: (0) todos los haces dispuestos en el centro del transcorte; (1) haces de 1° y 2° orden dispuestos en el centro del transcorte y haces de 3° orden desplazados hacia la cara abaxial.*

La posición de los haces vasculares en el transcorte y su patrón de distribución es un importante carácter diagnóstico (Ellis, 1976); sin embargo en algunas especies la proporción relativa de los diferentes haces varía desde la parte media de la lámina hacia el margen. Con la finalidad de que las observaciones fuesen comparables, los caracteres 21 y 22 fueron tomados en la porción media de cada una de las semiláminas.

23. *Relación entre los grupos de células buliformes y los haces vasculares de 3° orden: (0) células buliformes entre haces vasculares; (1) células buliformes sobre un haz de 3° orden; (2) células buliformes sobre tres o más haces de 3° orden.*

La ubicación de las células buliformes con respecto a los haces vasculares es un carácter que se asocia, en parte, al tipo fotosintético de la especie. Según Renvoize (1987b) en los géneros de la tribu Paniceae, fotosintéticamente C_4 NADP-me, subtipo MS, como *Axonopus*, *Anthaenantiopsis*, *Thrasya* y *Paspalum*, las células buliformes se ubican siempre sobre haces vasculares menores. A diferencia de esto, las células buliformes se ubican entre haces vasculares en *Panicum laxum*, especie fotosintéticamente C_3 y en *Eriochloa*, género que presenta tipo anatómico-fisiológico C_4 PCK, subtipo PS.

24. *Vaina mestomática: (0) sin cloroplastos; (1) con cloroplastos.*
25. *Vaina parenquimática: (0) sin cloroplastos; (1) con cloroplastos.*

Los caracteres 24 y 25 hacen referencia a características anatómicas que permiten inferir la vía fotosintética utilizada por las especies. Para establecer las homologías entre los tipos fotosintéticos se siguió el criterio de Brown (1977) y Dengler et al. (1985). Dichos autores homologan la vaina Kranz de las especies C_4 con subtipo anatómico MS, a la vaina interna de las especies C_4 con subtipo anatómico PS y a la vaina interna de las especies C_3 non-Kranz. En los tres casos estas vainas son mestomáticas por su origen ya que se generan del mismo meristema que origina al tejido vascular. A diferencia de ello, las especies C_4, anatómicamente PS, presentan la vaina Kranz en posición externa la cual se homologa a la vaina parenquimática de las especies C_3, pues en ambos casos estas vainas provienen del meristema fundamental juntamente con las células parenquimáticas del mesofilo.

26. *Vaina parenquimática: (0) ausente; (1) remanente; (2) presente.*

Morrone et al. (1993) mencionan en el género *Anthaenantiopsis* la presencia de algunas células por fuera de la vaina mestomática, de aspecto globoso y con paredes gruesas, con o sin cloroplastos especializados; dichas células son interpretadas por los autores como restos de una vaina parenquimática en proceso de reducción.

Los caracteres 24, 25 y 26 son características anatómicas asociadas a distintos procesos fotosintéticos y fueron considerados con el objeto de resolver relaciones entre los taxones externos, con lo cual se puede prevenir algunas topologías erróneas del grupo interno causadas por incorrectas resoluciones del grupo externo (Nixon & Carpenter, 1993).

27. *Células distintivas Kranz: (0) ausentes; (1) presentes.*

Dichas células presentan características ultraestructurales semejantes a las de la vaina mestomática Kranz. Se ubican solitarias o en pequeños grupos de dos o tres células entre haces vasculares contiguos, separados éstos por más de cuatro células clorenquimáticas; las células distintivas se conectan a los haces vasculares vecinos por medio de venillas transversales (Sánchez & Arriaga, 1989). Según Hattersley y Watson (1992) podrían interpretarse como reducciones extremas de haces vasculares de menor orden. Su presencia dentro del género *Paspalum* fue corroborada para los grupos Bonplandiana y Racemosa, anteriormente citadas por Cialdella et al. (1995) y Morrone et al. (1995) respectivamente.

28. *Células buliformes: (0) cubriendo casi toda la superficie; (1) en grupos definidos.*

Las células buliformes se presentan en la epidermis adaxial y pueden formar grupos regulares bien definidos con aspecto de abanico, dispuestos sobre uno a tres haces terciarios. En otros casos se distribuyen en casi toda la superficie, excepto sobre los haces mayores, diferenciándose de las restantes células epidérmicas solamente por ser de mayor tamaño.

29. *Grupos de células buliformes asociadas a tejido parenquimático incoloro: (0) ausentes; (1) presentes.*
30. *Parénquima incoloro dispuesto en las alas: (0) ausente; (1) presente.*

Este carácter hace referencia al parénquima incoloro asociado a los haces vasculares dispuestos en las alas, el cual puede formar en algunos casos proyecciones adaxiales y/o abaxiales con distinto grado de desarrollo. Queda excluido de este carácter el parénquima incoloro asociado a las células buliformes y la zona parenquimática de la costilla central.

31. *Pared tangencial externa de las células epidérmicas adaxiales: (0) recta; (1) convexa; (2) papilosa.*
32. *Pared tangencial externa de las células epidérmicas abaxiales: (0) recta; (1) convexa; (2) papilosa.*

Los caracteres 31 y 32 se refieren a las células epidérmicas observadas en corte transversal. Las mismas difieren en la forma que adquiere la pared tangencial externa, pudiendo ser totalmente recta (estado 0) o presentarse arqueada o convexa dando a la célula el aspecto de inflada (estado 1). Se consideró célula papilosa (estado 2) solamente cuando la pared tangencial externa se evagina notoriamente formando una protuberancia digitiforme.

33. *Macropelos adaxiales: (0) ausentes; (1) presentes.*
34. *Macropelos abaxiales: (0) ausentes; (1) presentes.*

La presencia de macropelos es un carácter muy frecuente en el género *Paspalum*; la mayoría de las especies poseen macropelos en una o ambas epidermis, pudiendo ser largos y muy abundantes o escasos y dispersos en la superficie. Son unicelulares, con paredes más o menos engrosadas, con la base bulbosa hundida en la epidermis, asociada en algunos casos a células epidérmicas sobreelevadas formando un cojín basal. Si bien los mismos presentan una marcada variación en cuanto a su longitud, frecuencia, espesor de la pared y ángulo de emergencia, sólo se consideraron aquellos aspectos más estables por

lo cual tales características no fueron incluidas en el análisis debido su variación intraespecífica.

35. Asperezas adaxiales: (0) ausentes; (1) presentes.
36. Asperezas abaxiales: (0) ausentes; (1) presentes.

El término aspereza se refiere a células epidérmicas con la pared tangencial externa aguda; las mismas pueden diferenciarse en aguijones o ganchos según el tamaño relativo entre el cuerpo de la célula y la proyección externa de la misma (Ellis, 1976). Dentro del género *Paspalum* se observaron formas intermedias por lo cual se reunió a ambos tipos dentro de un mismo carácter.

Apéndice 3. Matriz de datos. Referencias: [ ] indica carácter polimorfo; — indica carácter no comparable

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Panicum laxum	0	1	2	0	1	1	1	[01]	1	1	1	0	0	0	1	0	1	0
Eriochloa	0	0	0	0	1	0	0	1	1	1	1	0	0	0	1	0	0	0
Anthaenantiopsis	0	0	2	0	1	1	1	1	1	1	1	0	0	0	1	0	1	0
Axonopus	0	1	2	0	1	0	0	0	0	1	1	1	0	0	1	1	0	0
Thrasya	0	0	0	1	1	1	1	1	1	1	1	—	0	0	1	0	0	0
P. malacophyllum	0	0	2	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0
P. simplex	0	0	2	1	1	1	1	0	0	0	0	1	0	0	1	0	0	0
P. bertonii	0	0	1	1	0	1	0	1	0	1	1	0	0	0	1	2	1	0
P. lilloi	0	0	1	0	0	1	0	1	0	1	1	0	0	0	1	2	1	0
P. bonplandianum	0	1	2	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0
P. pallidum	0	1	2	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0
P. caespitosum	0	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. indecorum	0	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	1	0
P. polyphyllum	0	0	[12]	0	1	1	1	1	0	1	1	0	0	0	1	0	0	0
P. stellatum	0	0	[12]	1	0	1	0	1	0	1	1	0	0	0	1	0	1	0
p. conjugatum	0	1	1	0	0	1	0	1	0	1	1	1	0	0	1	0	0	0
P. corcovadense	0	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. mandiocanum	0	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. dilatatum	0	0	2	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0
P. urvillei	0	0	2	0	1	1	1	1	0	1	1	1	0	0	1	0	0	0
P. repens	0	1	2	1	0	1	0	1	0	1	1	1	0	0	1	0	1	1
P. distichum	0	1	1	0	0	1	0	[01]	[01]	1	1	1	0	0	1	0	1	1
P. vaginatum	0	1	1	0	0	1	0	[01]	0	1	1	1	0	0	1	0	1	0
P. gardnerianum	0	0	2	0	1	1	1	[01]	0	0	1	1	1	1	1	0	0	0
P. ammodes	0	0	2	0	0	1	0	1	0	1	1	1	0	0	1	1	0	0
P. erianthum	0	0	2	0	1	1	1	1	0	1	1	1	0	0	1	0	1	0
P. equitans	0	0	2	0	0	1	0	0	0	1	1	1	0	0	1	0	1	0
P. fasciculatum	0	1	2	0	0	1	0	0	[01]	1	1	1	0	0	1	0	1	0
P. filiforme	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0	4	—	—
P. lindnerianum	0	0	[01]	0	0	1	0	0	0	1	1	1	0	0	0	4	—	—
P. inaequivalve	0	1	2	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. lineare	0	0	[12]	0	0	1	0	[01]	0	1	1	1	0	0	0	3	—	—
P. proximum	0	0	[12]	0	0	1	0	[01]	0	1	1	1	0	0	1	1	0	0
P. alcalinum	0	0	2	0	1	1	1	[01]	0	1	1	1	0	0	1	0	0	0
P. lividum	0	1	2	1	1	1	1	[01]	0	1	1	1	0	0	1	0	0	0
P. macrophyllum	0	0	2	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. notatum	0	1	1	0	0	1	0	0	0	1	1	1	0	0	1	0	1	0
P. pumilum	0	0	1	0	0	1	0	0	[01]	1	1	1	0	0	1	0	0	0
P. orbiculatum	0	1	1	0	0	1	0	0	0	1	1	1	1	0	1	0	0	0
P. juergensii	0	0	2	0	1	1	1	[01]	0	1	1	1	0	0	1	0	0	0
P. paniculatum	0	0	2	0	1	1	1	[01]	0	1	1	1	0	0	1	0	0	0
P. crispatum	0	0	[12]	0	1	1	1	0	0	1	1	1	0	0	1	0	0	0
P. parviflorum	1	0	[12]	0	0	1	0	0	0	1	1	1	0	0	1	0	0	0
P. modestum	0	1	2	0	0	1	0	[01]	0	1	1	1	1	1	1	0	0	0
P. plicatulum	0	0	2	0	1	1	1	[01]	0	1	1	1	1	1	1	0	0	0
P. coryphaeum	0	1	2	0	1	1	1	[01]	0	1	1	1	[01]	0	1	0	0	1
P. quadrifarium	0	0	2	0	1	1	1	[01]	0	1	1	1	[01]	0	1	0	1	[01]
P. penicillatum	1	1	2	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0
P. pygmaeum	1	0	2	1	0	1	0	0	0	1	1	1	0	0	1	0	0	0
P. saccharoides	0	0	2	0	0	1	0	1	0	1	1	0	0	0	1	0	1	0
P. regnellii	0	0	2	0	1	1	1	[01]	0	1	1	1	1	1	1	0	0	0
P. virgatum	0	0	2	0	1	1	1	[01]	0	1	1	1	1	1	1	0	[01]	0

Apéndice 3. Extendido.

	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36
Panicum laxum	1	0	2	0	0	0	[01]	2	0	1	0	0	0	0	0	0	0	0
Eriochloa	0	0	0	0	0	0	1	2	0	1	0	0	0	1	[01]	0	1	1
Anthaenantiopsis	1	0	0	1	2	1	[01]	1	0	1	1	0	0	0	[01]	[01]	[01]	[01]
Axonopus	1	0	[01]	0	2	1	—	0	0	0	0	0	1	0	[01]	[01]	0	0
Thrasya	1	0	[01]	1	2	1	—	0	0	1	0	0	0	1	1	1	1	1
P. malacophyllum	1	0	1	0	2	1	—	0	0	0	0	0	0	1	1	1	1	1
P. simplex	[01]	0	1	0	2	1	—	0	0	0	0	0	0	1	1	1	1	1
P. bertonii	0	0	1	1	2	1	—	0	0	1	0	1	2	0	0	0	0	0
P. lilloi	0	0	1	1	2	1	—	0	0	1	0	1	2	0	0	0	0	0
P. bonplandianum	[01]	0	0	0	1	1	—	0	1	1	0	0	1	1	1	1	[01]	[01]
P. pallidum	[01]	0	0	0	1	1	—	0	1	0	0	0	1	1	1	1	0	0
P. caespitosum	1	0	0	1	1	1	—	0	0	1	0	0	0	0	[01]	[01]	1	1
P. indecorum	1	0	1	1	2	1	—	0	0	1	0	0	0	2	1	1	1	1
P. polyphyllum	1	0	1	0	2	1	—	0	0	0	0	0	2	2	1	1	0	0
P. stellatum	1	0	1	1	2	1	—	0	0	1	0	0	1	0	1	1	[01]	[01]
P. conjugatum	1	0	1	0	2	1	—	0	0	0	0	0	1	0	[01]	[01]	0	0
P. corcovadense	1	0	[01]	1	[12]	1	0	0	0	1	0	0	0	1	[01]	1	[01]	1
P. mandiocanum	1	0	[01]	[01]	[12]	1	—	0	0	1	0	0	0	1	[01]	1	1	1
P. dilatatum	1	0	1	1	1	1	—	0	0	1	0	0	1	1	0	[01]	1	1
P. urvillei	1	0	1	1	1	1	—	0	0	1	0	0	1	1	0	0	1	1
P. repens	1	1	0	0	1	1	—	0	0	1	0	0	2	2	1	1	1	1
P. distichum	0	0	0	1	1	1	—	0	0	1	0	0	2	2	0	0	0	0
P. vaginatum	0	0	0	1	1	1	—	0	0	1	0	[01]	2	0	0	0	[01]	[01]
P. gardnerianum	[01]	0	[01]	0	[12]	1	—	0	0	1	0	0	1	1	[01]	[01]	1	[01]
P. ammodes	1	0	0	1	1	1	—	0	0	1	0	0	1	1	1	1	1	1
P. erianthum	1	0	[01]	[01]	[12]	1	—	0	0	1	0	0	1	0	[01]	[01]	1	[01]
P. equitans	1	0	[01]	1	[12]	1	—	0	0	1	0	0	2	0	0	0	0	[01]
P. fasciculatum	1	0	[01]	1	[12]	1	—	0	0	1	0	0	0	0	0	0	1	[01]
P. filiforme	1	0	—	—	—	1	—	0	0	1	0	0	0	0	0	0	1	1
P. lindnerianum	1	0	—	—	—	1	—	0	0	1	0	0	0	0	0	0	1	0
P. inaequivalve	1	0	0	0	1	1	0	0	0	1	0	0	0	0	[01]	[01]	[01]	[01]
P. lineare	1	0	—	—	—	1	—	0	0	—	—	—	—	0	—	0	—	0
P. proximum	1	0	0	1	—	1	—	0	0	—	—	1	2	0	0	0	[01]	0
P. alcalinum	1	[01]	1	1	1	1	—	0	0	1	0	0	1	2	1	1	1	1
P. lividum	1	[01]	1	0	2	1	—	0	0	1	0	0	1	2	1	1	1	1
P. macrophyllum	1	0	1	0	2	1	—	0	0	1	0	0	1	1	0	0	[01]	[01]
P. notatum	[01]	0	0	1	1	1	—	0	0	1	0	0	0	0	[01]	[01]	1	0
P. pumilum	[01]	0	[01]	1	[12]	1	—	0	0	1	0	0	0	1	1	1	[01]	[01]
P. orbiculatum	0	0	0	0	1	1	—	0	0	1	0	0	1	1	[01]	[01]	0	0
P. juergensii	1	0	0	0	1	1	—	0	0	1	0	0	0	1	[01]	[01]	1	1
P. paniculatum	[01]	0	0	0	1	1	—	0	0	1	0	0	0	1	[01]	0	1	1
P. crispatum	1	0	1	0	2	1	—	0	0	0	0	0	2	2	1	1	1	[01]
P. parviflorum	[01]	0	1	1	2	1	—	0	0	0	0	0	1	1	1	1	[01]	0
P. modestum	1	1	0	1	1	1	—	0	0	1	0	0	1	1	0	0	0	0
P. plicatulum	1	0	1	1	2	1	—	0	0	1	0	0	1	1	[01]	[01]	1	1
P. coryphaeum	[01]	0	1	1	2	1	—	0	0	0	0	0	1	1	1	1	1	1
P. quadrifarium	1	0	0	1	1	1	—	0	0	1	0	0	1	1	0	0	1	1
P. penicillatum	1	0	0	0	1	1	—	0	1	0	0	0	1	1	[01]	[01]	0	0
P. pygmaeum	[01]	0	0	0	1	1	—	0	1	0	0	0	1	1	1	1	0	0
P. saccharoides	0	0	[01]	1	[12]	1	—	0	0	1	0	0	2	0	1	0	1	0
P. regnellii	[01]	0	0	0	1	1	—	0	0	1	0	0	1	1	0	[01]	1	1
P. virgatum	1	[01]	0	1	1	1	—	0	0	1	[01]	0	1	1	[01]	0	[01]	0

GOCHNATIA (ASTERACEAE, MUTISIEAE) AND THE *GOCHNATIA* COMPLEX: TAXONOMIC IMPLICATIONS FROM MORPHOLOGY[1]

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Abstract

Gochnatia is one of the largest genera of the tribe Mutisieae (Asteraceae) and has been traditionally characterized by its homogamous capitula with isomorphic corollas. A morphological study of *Gochnatia* and associated genera, i.e., *Actinoseris*, *Chucoa*, *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, *Pleiotaxis*, and *Wunderlichia*, was carried out to evaluate the circumscription of *Gochnatia* and its sections, and the affinities of this complex of genera. The characters studied involve habit, leaf features (consistency, pubescence type, shape, margin, and venation), types of capitulescence, involucre features (shape, size, phyllary series, pubescence, and shape), paleae, floret features (morphology, sex, number, color of corolla, anthers, style shapes, achenial pubescence, and pappus). Analysis of these features revealed: (1) although *Gochnatia* is highly variable in most of the characters studied, it can be defined by this suite of features: isomorphic to subdimorphic corollas, apiculate anther appendages, and smooth style branches; (2) sections of *Gochnatia* needed to be re-evaluated. As result of this, two sections, i.e., sect. *Discoseris* and sect. *Pentaphorus*, are confirmed; two sections are proposed, i.e., sect. *Glomerata* sect. nov. and sect. *Rotundifolia* sect. nov.; three sections are redefined, i.e., sect. *Hedraiophyllum*, sect. *Leucomeris*, and sect. *Gochnatia*, while sect. *Anastraphioides* is formally published; and (3) the combination of apiculate anther appendages and smooth style branches is unique to *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Gochnatia*, *Hyalis*, *Ianthopappus*, and *Nouelia* within the Mutisieae. This group of genera is recognized here as the *Gochnatia* complex, with *Gochnatia* as the basal genus of this complex. *Chucoa*, *Pleiotaxis*, and *Wunderlichia* do not belong to the *Gochnatia* complex.

Key words: Asteraceae, Compositae, *Gochnatia*, *Gochnatia* complex, infrageneric classification, morphology, Mutisieae.

Gochnatia Kunth is one of the largest genera of the tribe Mutisieae, subtribe Mutisiinae sensu lato (including Gochnatiinae; Robinson, 1991; Bremer, 1994). It comprises 68 species, nearly all Neotropical and 2 endemic to the mountains of southeastern Asia. All the species of *Gochnatia* have been traditionally described as discoid with actinomorphic, deeply 5-lobed corollas, features that are plesiomorphic within Mutisieae (Bremer, 1994). The only apomorphic character suggested for the genus is the acuminate to apiculate apical anther appendage of the stamens (Bremer, 1994). This character, however, is shared by other genera of Mutisieae.

The infrageneric taxonomy of *Gochnatia* has been much discussed (Lessing, 1832; de Candolle, 1838; Jervis, 1954; Cabrera, 1971) since the genus was established by Kunth (1818). Cabrera (1971), in his monograph of the genus, divided it into six sections: sect. *Discoseris*, sect. *Gochnatia*, sect. *Hedraiophyllum*, sect. *Leucomeris*, sect. *Moquiniastrum*, and sect. *Pentaphorus*. He suggested the artificial delimitation of some sections, such as *Hedraiophyllum*, and in other cases emphasized geographical distribution in distinguishing groups of species, such as in section *Gochnatia*.

Jeffrey (1967), when relating *Gochnatia* to other taxa, established the *Stifftia*-series of genera, which all have short, rounded, glabrous style arms, and commonly glabrous corollas. The *Stifftia*-series was then divided into four subseries by slight differences in the shape of the style arms, although these

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differences were not described for each subseries. Of these subseries, the *Gochnatia*-subseries included *Achnopogon, Cnicothamnus, Gochnatia, Nouelia,* and *Oldenburgia.*

Cabrera (1971) considered *Actinoseris, Cyclolepis,* and *Pleiotaxis* closely related to *Gochnatia* by their apiculate anthers. Later, he also associated *Chucoa* with *Gochnatia* (Cabrera, 1977). Hansen (1991) considered only *Actinoseris* and *Cyclolepis* of Cabrera's group to be close to *Gochnatia,* excluding *Pleiotaxis* and *Chucoa,* and added *Hyalis* and *Nouelia* to what he called the "*Gochnatia*-group." Hansen argued the presence of cone-like involucres, i.e., with light brownish bracts imbricately arranged and resembling the cone of a spruce as a probable synapomorphy of the group. Recently, Roque and Hind (2001) created the new genus *Ianthopappus* for the species *Actinoseris corymbosa.* In this work, the authors grouped the genera *Actinoseris, Chucoa, Cnicothamnus, Cyclolepis, Gochnatia, Hyalis, Ianthopappus,* and *Nouelia* by their apiculate to acuminate apical anther appendages. Furthermore, Roque (2001) and Roque and Pirani (2001) re-circumscribed the genus *Richterago* Kuntze according to the genus concept first employed by Lessing (1830) to include the species of *Actinoseris* and the species of *Gochnatia* sect. *Discoseris.* We consider, however, that the characters used to distinguish *Richterago* are widespread in *Gochnatia* or are shared with other genera, such as herbaceous to subshrubby habit (shared among *Gochnatia* sect. *Discoseris, Actinoseris,* and other such related genera as *Hyalis* and *Ianthopappus*), leaves rosulate to alternate (alternate leaves are present in most species of *Gochnatia*), venation pinnate (present in most species of *Gochnatia*), capitula homogamous and discoid (present in most species of *Gochnatia*) or heterogamous and radiate (present in some species of *Actinoseris*), as well as pappus features, i.e., pappus uniseriate, with 25 to 42 bristles, united into a fleshy ring (present in species of *Gochnatia* sect. *Gochnatia*). For these reasons, we affirm here the traditional concept of *Gochnatia* and *Actinoseris* (excluding *A. corymbosa* = *Ianthopappus corymbosus*) as was established by Cabrera (1970, 1971).

Some phylogenetic studies relate *Gochnatia* with other genera of Mutisieae; for example, Jansen and Palmer (1987) related *Gochnatia* with *Ainsliaea, Onoseris,* and *Stifftia,* and Karis et al. (2001) related it with *Mutisia* and *Trixis.* However, because of the few taxa sampled in the tribe, these analyses are not considered here to address relationships at the generic level.

In other analyses (Karis et al., 1992; Jansen & Kim, 1996), *Gochnatia* was found to be an isolated taxon within Cichorioideae. The cladogram of Karis et al. (1992), based on morphological characters, shows *Gochnatia* as sister to most Asteraceae, excluding Barnadesioideae and four genera of Gochnatiinae. The *ndh*F tree of Jansen and Kim (1996) also shows *Gochnatia* as an independent lineage positioned basal to most Asteraceae, excluding Barnadesioideae and the core of Mutisieae examined. There are other genera within Mutisieae such as *Quelchia* and *Neblinaea* from the Guayana Highland with apiculate anther appendages, but morphological features of these genera (Pruski, 1991; Bremer, 1994) mark a departure from *Gochnatia* and associated taxa. On the other hand, the planaltive Brazilian genus *Wunderlichia,* with shortly apiculate anther appendages, was either placed in the "*Stenopadus* group" (Pruski, 1991) or it was considered isolated within Mutisieae (Hansen, 1991; Karis et al., 1992; Bremer, 1994).

The group selected here for the analysis is mainly represented by the genera with apiculate anther appendages suggested by Jeffrey (in part, 1967), Cabrera (1971, 1977), Hansen (1991), and Roque and Hind (2001). It is comprised of *Actinoseris* sensu Cabrera, excluding *A. corymbosa* (7 species), *Chucoa* (1 species), *Cnicothamnus* (2 species), *Cyclolepis* (1 species), *Gochnatia* (68 species), *Hyalis* (2 species), *Ianthopappus* (1 species), *Nouelia* (1 species), *Pleiotaxis* (ca. 25 species), and the controversial *Wunderlichia* (6 species).

There are several potential diagnostic features in *Gochnatia* and relatives such as the habit, leaf morphology, types of capitulescence, involucre, florets, trichomes, and pappus that have never been studied comparatively or in detail. A detailed morphological study of *Gochnatia* and its associated taxa is needed as a first step to provide a robust base for discussion.

On the basis of morphological evidence, the goals of this study are: (1) to evaluate the circumscription of *Gochnatia* and its sections, and (2) to group *Gochnatia* with other genera based on their similarities.

Material and Methods

Herbarium specimens of the studied taxa, i.e., *Actinoseris, Chucoa, Cnicothamnus, Cyclolepis, Gochnatia* (64 of its 68 species), *Hyalis, Ianthopappus, Nouelia, Pleiotaxis,* and *Wunderlichia* (Appendix 1), were examined to assess characters used previously to distinguish taxa in this group of genera, and to search for additional characters. The data were augmented by literature studies (Fran-

chet, 1888; Cabrera, 1950, 1951, 1955, 1970, 1971; Jeffrey, 1967; Barroso & Maguire, 1973; Zardini, 1975; Sancho, 1997, 2000; Roque, 1997; Roque & Hind, 2001; Roque & Pirani, 1997, 2001).

Vegetative and floral parts were dissected and observed after boiling in water and stained with 2% safranin. Freehand sections of leaves were performed and these sections examined to determine the presence of hypodermis, and then stained with safranin. Drawings were made by the authors using a stereomicroscope Wild M5 and a microscope Leitz SM Lux with the camera lucida technique.

Apical anther appendages were described and drawn to include the portion ranging from the thecae apex to the apex of the stamen.

Descriptive terminology for the trichomes follows Ramayya (1962). Whenever possible, additional synonyms of trichome terminology were added (Payne, 1978; Font Quer, 1979; Moreno, 1984; Harris & Harris, 1994; Metcalfe & Chalk, 1950). Some authors use the term "trichome," whereas others apply the term "hair" in their pubescence classifications. Both terms are cited here following each author classification.

Results

For comparison with our results, sections of *Gochnatia* with their corresponding species according to Cabrera (1971) are listed in Table 1.

Vegetative characters

Habit. Taxa under study display four types of habit: small trees, shrubs, subshrubs, and perennial herbs. Several species of *Gochnatia* (e.g., *G. arborescens, G. decora, G. elliptica, G. ilicifolia, G. magna, G. oligocephala, G. palosanto, G. polymorpha, G. spectabilis, G. tortuensis*), *Cnicothamnus*, and *Wunderlichia* are small trees. Most species of *Gochnatia, Chucoa, Cyclolepis*, and *Nouelia* are shrubs. *Gochnatia* sect. *Discoseris, Hyalis*, and *Ianthopappus* are subshrubs. *Actinoseris* and *Pleiotaxis* are perennial herbs. *Cyclolepis* is the only spinose genus and is aphyllous at maturity.

Leaves. All taxa analyzed have alternate, occasionally rosulate, subsessile to shortly petiolate leaves.

Leaf consistency: The leaves are coriaceous or subcoriaceous, but only some species have leaves with an adaxial hypodermis. It is absent in some species of *Gochnatia* (e.g., *G. amplexifolia, G. arequipensis, G. cardenasii, G. discoidea, G. foliolosa, G. glutinosa, G. hypoleuca, G. intertexta, G. magna, G. palosanto, G. purpusii, G. rotundifolia, G. vernonioides*), *Actinoseris, Cnicothamnus, Cyclolepis, Hyalis, Ianthopappus*, and in some species of *Pleiotaxis* (e.g., *P. eximia, P. huillensis*). Occasionally, the hypodermis is discontinuous (e.g., *Gochnatia argentina, G. discolor, G. orbiculata, G. ramboi*).

Leaf shape: The leaves are always simple in the taxa under study, but show great variation in shape, from linear to suborbicular. Most species of *Gochnatia* sect. *Gochnatia* and *Nouelia* have leaves ovate to ovate-elliptic, obtuse to subobtuse at the apex; occasionally ovate leaves are acute at the apex (e.g., *G. polymorpha, G. vernonioides*), or cordate at the base (e.g., *G. cordata, G. haumaniana*) (Fig. 1A). Most of the Caribbean species of *Gochnatia* sect. *Gochnatia, Actinoseris* (*A. hatschbachii, A. polymorpha, A. radiata*), *Chucoa, Ianthopappus*, and *Wunderlichia* have obovate leaves (Fig. 1B). Elliptic leaves (Fig. 1C) are rounded in the base and apex in *G. discoidea*, attenuate at the base and apex in *G. magna, G.* sect. *Leucomeris, Actinoseris* (*A. polyphylla*), *Cnicothamnus*, and some species of *Pleiotaxis* (e.g., *P. huillensis, P. newtonii, P. selina, P. subscaposa*). *Gochnatia* sect. *Pentaphorus, G. argyrea, Actinoseris* (*A. angustifolia, A. stenophylla*), *Cyclolepis, Hyalis*, and most species of *Pleiotaxis* (e.g., *P. ambigua, P. decipiens, P. dewevrei, P. linearifolia, P. rogersii*) have linear leaves (Fig. 1D).

Leaf margin: Only the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. crassifolia* and *G. picardae*) and *Chucoa* have spinose margins (Fig. 1E). In the remaining taxa the leaf margin is predominantly entire or denticulate (Fig. 1F).

Leaf venation: The venation is predominantly pinnate, although in taxa such as *Gochnatia arequipensis, G. glutinosa, G. rotundifolia, Hyalis*, and *Ianthopappus* the leaves are three-veined (actinodromous).

Capitulescence

Capitula are borne singly or 2 or 3 at the end of the branches or may be clustered in pseudocorymbs, pseudoracemes, or pseudopanicles, in open to condensed or glomerulose synflorescences depending upon the length of the peduncles.

Solitary or few capitula (2 or 3) are short-pedunculate to glomerulose in *Gochnatia* sect. *Gochnatia, Cnicothamnus, Nouelia*, and some species of *Wunderlichia* (*W. azulensis, W. crulsiana, W. mirabilis*) (Fig. 2A). They are scapiform, long-pedunculate in *Gochnatia suffrutescens*, some species of *Actinoseris* (e.g., *A. angustifolia, A. hatschbachii, A. polymorpha, A. radiata*), *Chucoa*, and some species of *Pleiotaxis* (e.g., *P. subscaposa*) (Fig. 2B).

Table 1. Sections within *Gochnatia* established in this study on the basis of the morphology, compared with the sections delimited by Cabrera (1971), with the addition of *G. hatschbachii* (Cabrera, 1974) and *G. densicephala* (Sancho, 2000). The geographic distribution and diagnostic characters for each section are provided, with uncommon features appearing in parentheses. * = type species of each section.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
Gochnatia sect. *Discoseris*	*Gochnatia* sect. *Discoseris*		Subshrubs; capitula solitary, long-pedunculate, or numerous in scapose pseudocorymbs; appendage abruptly apiculate, laciniate tails; pappus type A
G. amplexifolia (Gardner) Cabrera	*G. amplexifolia*	Brazil	
**G. discoidea* (Less.) Cabrera	*G. discoidea*	Brazil	
G. suffrutescens Cabrera	*G. suffrutescens*	Brazil	
Gochnatia sect. *Gochnatia*	*Gochnatia* sect. *Gochnatia*		
South American species:			
G. arequipensis Sandw.	*G. arequipensis*	Peru	Leaves pinnately (subthree-) veined; solitary capitula (2 or 3); anther appendage caudate (abruptly apicualte), laciniate tails; pappus type B
G. boliviana S. F. Blake	*G. boliviana*	Bolivia	
G. cardenasii S. F. Blake	*G. cardenasii*	Bolivia	
G. curviflora (Griseb.) O. Hoffm.	*G. curviflora*	S Bolivia, NW Argentina	
G. patazina Cabrera	*G. patazina*	Peru	
G. vargasii Cabrera	*G. vargasii*	Peru	
**G. vernonioides* Kunth	*G. vernonioides*	N Peru	
	Gochnatia sect. *Rotundifolia*		
G. rotundifolia Less.	**G. rotundifolia*	S Brazil	Leaves three-veined, glabrous; solitary capitula; involucre with subglabrous phyllaries, ciliolate at the margins; corollas white; anther appendage attenuate, laciniate tails; pappus type B
Caribbean species:	*Gochnatia* sect. *Anastraphioides*		
G. attenuata (Britton) Jervis & Alain	*G. attenuata*	Cuba	Leaves with spinose (entire) margin; solitary capitula (2 or 3); corollas deeply to very deeply 5-lobed; anther appendage caudate (abruptly apiculate), smooth tails (laciniate); capitate glandular hairs in achenes; pappus type A (type B)
G. buchii (Urb.) Jiménez	*G. buchii*	Caribbean	
G. calcicola (Britton) Jervis & Alain	*G. calcicola*	Cuba	
G. cowellii (Britton) Jervis & Alain	*G. cowellii*	Cuba	
G. crassifolia (Britton) Jervis & Alain	*G. crassifolia*	Cuba	
G. cubensis (Carabia) Jervis & Alain	*G. cubensis*	Cuba	
G. ekmanii (Urb.) Jervis & Alain	*G. ekmanii*	Cuba	
G. elliptica (León) Alain	*G. elliptica*	Cuba	
G. enneantha (S. F. Blake) Alain	*G. enneantha*	Dominican Republic	
G. gomezii (León) Jervis & Alain	*G. gomezii*	Cuba	
G. ilicifolia Less.	**G. ilicifolia*	Caribbean	

Table 1. Continued.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
G. intertexta (Griseb.) Jervis & Alain	*G. intertexta*	Cuba	
G. maisiana (León) Jervis & Alain	*G. maisiana*	Cuba	
G. mantuensis (Griseb.) Jervis & Alain	*G. mantuensis*	Cuba	
G. microcephala (Griseb.) Jervis & Alain	*G. microcephala*	Cuba	
G. montana (Britton) Jervis & Alain	*G. montana*	Cuba	
G. obtusifolia (Britton) Jervis & Alain	*G. obtusifolia*	Cuba	
G. oligantha (Urb.) Howard	*G. oligantha*	Caribbean	
G. parvifolia (Britton) Jervis & Alain	*G. parvifolia*	Cuba	
G. pauciflosculosa (Hitchc.) Cabrera	*G. pauciflosculosa*	Bahamas	
G. picardae (Urb.) Jiménez	*G. picardae*	Haiti	
G. recurva (Britton) Jervis & Alain	*G. recurva*	Cuba	
G. sagraeana Jervis & Alain	*G. sagraeana*	Cuba	
G. shaferi (Britton) Jervis & Alain	*G. shaferi*	Cuba	
G. tortuensis (Urb.) Jiménez	*G. tortuensis*	Haiti	
G. wilsonii (Britton) Jervis & Alain	*G. wilsonii*	Cuba	
Gochnatia sect. *Hedraiophyllum*	*Gochnatia* sect. *Glomerata*		
G. arborescens T. S. Brandegee	**G. arborescens*	Mexico	Capitula few together in glomerulose pseudocorymbs; florets 12 to 20(50); anther appendage abruptly apiculate (attenuate), smooth tails; pappus type B (type A)
**G. cordata* Less.	(moved to another section)		
G. magna Cabrera	*G. magna*	Mexico	
G. purpusii T. S. Brandegee	*G. purpusii*	Mexico	
	Gochnatia sect. *Leucomeris*		
G. hypoleuca (DC.) A. Gray	*G. hypoleuca*	S U.S.A., Mexico	Numerous capitula in glomerulose pseudocorymbs, pseudoracemes or pseudopanicles; involucre with glabrous, ciliolate at the margin phyllaries extending into the peduncle; florets 4 to 6(8 to 12), white (yellow); anther appendage attenuate (abruptly apiculate), laciniate tails (smooth); pappus type B
G. palosanto Cabrera	*G. palosanto*	N Argentina, S Bolivia	
G. smithii Robinson & Greenm.	*G. smithii*	Mexico	

Table 1. Continued.

Sections sensu Cabrera (1971)	Sections according to this study	Distribution	Diagnostic characters
Gochnatia sect. *Leucomeris*			
G. decora (Kurz) Cabrera	*G. decora*	Asia	
**G. spectabilis* (D. Don) Less	*G. spectabilis*	Asia	
Gochnatia sect. *Moquiniastrum*	*Gochnatia* sect. *Hedraiophyllum*		
G. argentina (Cabrera) Cabrera	*G. argentina*	N Argentina	
G. argyrea (Malme) Cabrera	*G. argyrea*	S Brazil	Trees or shrubs, gynodioecious, polygamous (monoecious); leaves with 2-, 3- to 5-armed (flagellate) hairs; numerous capitula in glomerulose to loose pseudopanicles; capitula heterogamous (homogamous), disciform (discoid); corollas subdimorphic (isomorphic); anther appendage abruptly apiculate, laciniate, smooth tails; pappus type C
G. barrosii Cabrera	*G. barrosii*	S Brazil, Paraguay	
G. blanchetiana (DC.) Cabrera	*G. blanchetiana*	E Brazil	
	**G. cordata* Less.	Paraguay, Brazil, Uruguay, Argentina	
	G. densicephala (Cabrera) G. Sancho	E Brazil	
G. discolor Baker	*G. discolor*	Brazil	
G. floribunda Cabrera	*G. floribunda*	Brazil	
G. gardneri (Baker) Cabrera	*G. gardneri*	Brazil	
	G. hatschbachii Cabrera	Brazil	
G. haumaniana Cabrera	*G. haumaniana*	Paraguay, Brazil	
G. mollissima (Malme) Cabrera	*G. mollissima*	S Brazil	
G. oligocephala (Gardner) Cabrera	*G. oligocephala*	E Brazil	
G. orbiculata (Malme) Cabrera	*G. orbiculata*	E Brazil	
G. paniculata (Less.) Cabrera	*G. paniculata*	SE Brazil	
G. polymorpha (Less.) Cabrera	*G. polymorpha*	Brazil, Paraguay, Uruguay, Argentina	
G. pulchra Cabrera	*G. pulchra*	S Brazil, Paraguay	
G. ramboi Cabrera	*G. ramboi*	S Brazil	
G. rusbyana Cabrera	*G. rusbyana*	Andes of Peru, Bolivia	
G. sordida (Less.) Cabrera	*G. sordida*	S Brazil	
G. velutina (Bong.) Cabrera	*G. velutina*	S Brazil	
Gochnatia sect. *Pentaphorus*	*Gochnatia* sect. *Pentaphorus*		Linear leaves, pinnately, three-veined, glandulate; numerous capitula in glomerulose, leafy pseudoracemes; florets 5 (3, 7, or 10 to 20), white or lilac; anther appendage abruptly apiculate, smooth, laciniate tails; pappus type D
**G. foliolosa* (D. Don) Hook. & Arn.	*G. foliolosa*	Central Chile	
G. glutinosa (D. Don) Hook & Arn.	*G. glutinosa*	W Argentina	

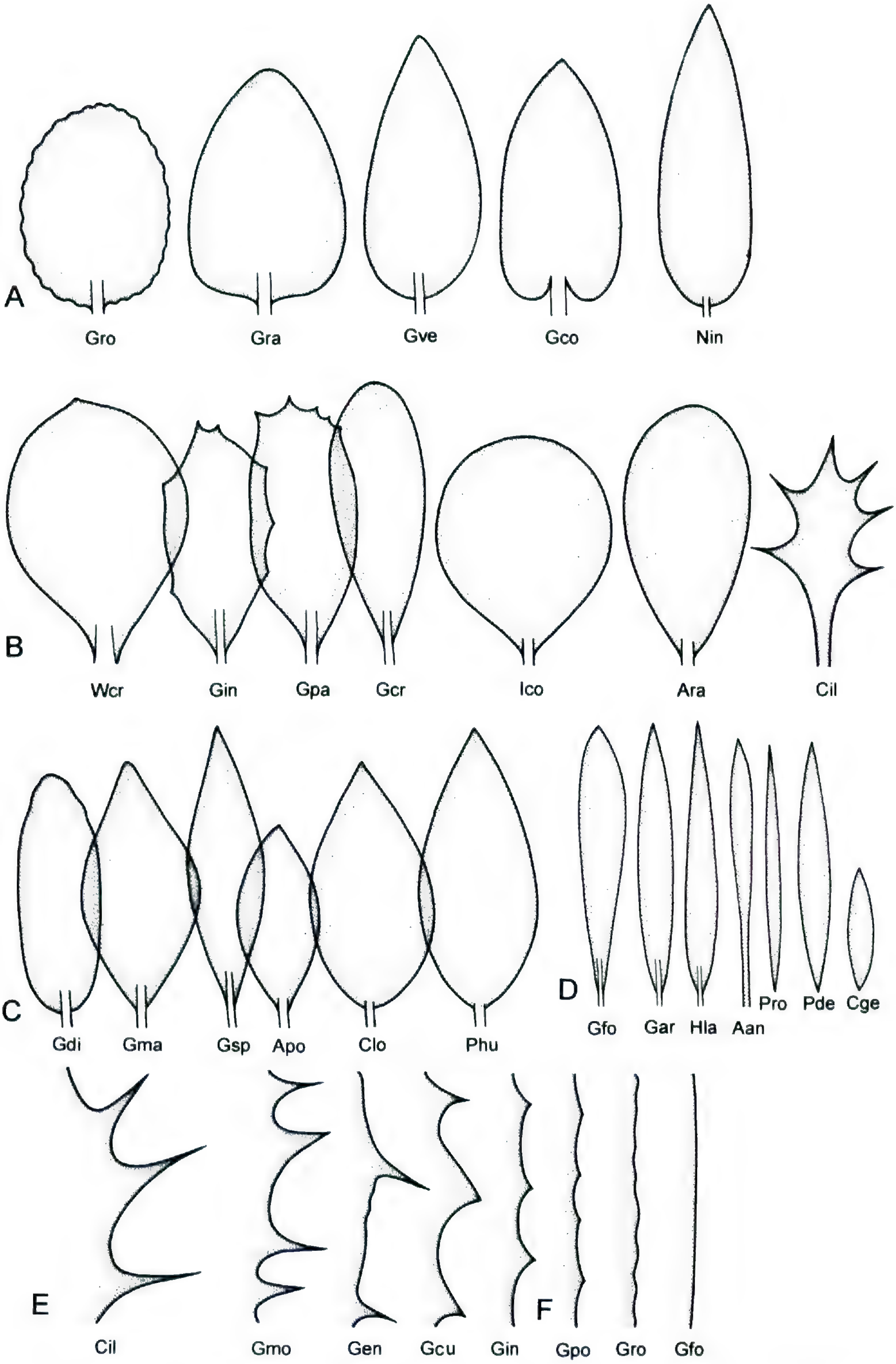

Figure 1. Leaf shape. —A. Ovate (left to right): *Gochnatia rotundifolia* (*Handro 157*, LP), *G. ramboi* (*Rambo 50005*, S), *G. vernonioides* (*López & Sagástegui 3354*, LP), *G. cordata* (*Serrano 6*, LP), *Nouelia insignis* (*l'Abbé Delavay 2498*, US). —B. Obovate (left to right): *Wunderlichia crulsiana* (*Ratter et al. 2615*, MO), *Gochnatia intertexta* (*Alain A-1680*, NY), *G. paucifloscculosa* (*Wilson 7428*, K), *G. crassifolia* (*Ekman 4023*, S), *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304*, LP), *Actinoseris radiata* (*Hatschbach 690*, LP), *Chucoa ilicifolia* (*López Miranda 1090*, LP). —C. Elliptic (left to right): *Gochnatia discoidea* (*Blanchet 3345*, LP), *G. magna* (*Cronquist 11277*, NY), *G. spectabilis* (*Galrola 32*, LP),

Few to several capitula (more than 4) arranged in short-pedunculate to glomerulose pseudocorymbs are found in *Gochnatia arborescens, G. magna, G. purpusii, Gochnatia* sect. *Leucomeris, Hyalis lancifolia,* and *Wunderlichia* (*W. bahiensis, W. insignis*) (Fig. 2C). Numerous capitula arranged in scapiform, long-pedunculate pseudocorymbs are found in *Gochnatia* sect. *Discoseris* (except *G. suffrutescens*), *Actinoseris* (*A. stenophylla*), *Hyalis argentea, Ianthopappus,* and *Wunderlichia senaeii* (Fig. 2D).

Gochnatia sect. *Pentaphorus* and *Cyclolepis* have numerous capitula borne in short-pedunculate to glomerulose clusters, that are in turn arranged in leafy pseudoracemes (Fig. 2E). Pseudoracemes in compact or glomerulose clusters, which lack leaves, at the tip of the branches, are characteristic of *Gochnatia palosanto* (Fig. 2F). Loose pseudoracemes are present only in some species of *Pleiotaxis* (e.g., *P. angusterugosa, P. gombensis, P. oxylepis, P. racemosa*) (Fig. 2G).

Numerous capitula arranged in glomerulose pseudopanicles are present in most species of *Gochnatia* sect. *Moquiniastrum,* in *G. cordata, G. hypoleuca,* and *G. smithii* (Fig. 2H). Short-pedunculate (Fig. 2I) or loose pseudopanicles (Fig. 2J) are present in species of *Gochnatia* sect. *Moquiniastrum* (*G. argentina, G. argyrea,* respectively).

INVOLUCRE

Shape. The involucre shape is either oblong to campanulate or turbinate. Oblong to campanulate involucres are characteristic of most species of *Gochnatia* (Fig. 3A), *Chucoa* (Fig. 3B), *Cnicothamnus* (Fig. 3C), *Cyclolepis* (Fig. 3D), *Hyalis* (Fig. 3E), *Nouelia* (Fig. 3F), *Pleiotaxis* (Fig. 3G), and *Wunderlichia* (Fig. 3H). Turbinate involucres, on the other hand, occur in a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cubensis, G. intertexta, G. pauciflosculosa*), in some species of *G.* sect. *Hedraiophyllum* (*G. hypoleuca, G. palosanto, G. smithii*) (Fig. 3I), *G. suffrutescens, Actinoseris,* and *Ianthopappus* (Fig. 3J).

Size. The involucre size ranges from 2 to 45 mm high, with three main categories: (2–)4–7(–8) mm, 10–18 mm, and 20–45 mm high.

(A) The smallest involucres [(2–)4–7(–8) mm] are present in *Gochnatia* sect. *Pentaphorus, Gochnatia* sect. *Moquiniastrum* (except *G. argyrea* with 9–10 mm), *G. hypoleuca, G. microcephala, G. palosanto, G. smithii, Cyclolepis,* and *Hyalis.*

(B) Intermediate involucres (10–18 mm high) are present in some species of *Gochnatia* (e.g., *G. arborescens, G. cordata, G. discoidea, G. ilicifolia, G. magna, G. patazina, G. purpusii, G. recurva, G. rotundifolia, G. vernonioides*), *Actinoseris, Chucoa,* and *Ianthopappus.*

(C) The biggest involucres (20–45 mm) are displayed by a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cowellii, G. cubensis, G. ekmanii, G. picardae, G. sagraeana*), *Cnicothamnus, Nouelia, Pleiotaxis,* and *Wunderlichia.*

Series of phyllaries. The phyllaries are arranged in several imbricate series. The highest number is (6)7 to 10 series, and this is found in a few Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. cowellii, G. cubensis, G. picardae, G. recurva*), *G. arborescens, Cnicothamnus* (Fig. 3C), *Nouelia* (Fig. 3F), *Pleiotaxis* (Fig. 3G), and *Wunderlichia* (Fig. 3H). Three- to six-seriate involucres occur in most species of *Gochnatia* (Fig. 3A), and *Actinoseris, Chucoa* (Fig. 3B), *Cyclolepis* (Fig. 3D), *Hyalis* (Fig. 3E), and *Ianthopappus* (Fig. 3J). *Gochnatia* sect. *Leucomeris* and three species of *G.* sect. *Hedraiophyllum* (*G. hypoleuca, G. palosanto, G. smithii*) show a peculiar feature in their involucres. The capitula are 3- to 4-seriate, but the peduncle bracts extend into the involucre giving a 7- to 12-seriate condition (Fig. 3I).

Phyllary pubescence and shape. In almost all the taxa studied the phyllaries are dorsally pubescent or subglabrous. However, *Gochnatia* sect. *Leucomeris, G. hypoleuca, G. palosanto, G. smithii,* and *G. rotundifolia* have dorsally glabrous phyllaries with ciliate margins.

Most genera have linear to oblong or obovate phyllaries with entire margins. *Cnicothamnus* has phyllaries with an apical appendage rounded or rhombic, with lacerate margins (Fig. 3C), and *Wunderlichia* has phyllaries with scarious, colored, and occasionally fimbriate margins (Fig. 3H).

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Actinoseris polyphylla (*Hatschbach 35304,* LP), *Cnicothamnus lorentzii* (*Padaci 84,* LP), *Pleiotaxis huillensis* (*Gossweiler 10780,* US). —D. Linear (left to right): *Gochnatia foliolosa* (*Cabrera 3451,* LP), *G. argyrea* (*Hatschbach 9578,* LP), *Hyalis lancifolia* (*Schinini 16098,* LP), *Actinoseris angustifolia* (*Hatschbach 29986,* LP), *Pleiotaxis rogersii* (*Rolyns 1568,* US), *P. dewevrei* (*de Hitte 288,* US), *Cyclolepis genistoides* (*Rojas 7104,* LP). Leaf margin. —E. Spinose (left to right): *Chucoa ilicifolia* (*López Miranda 1090,* LP), *Gochnatia montana* (*Ekman 18725,* S), *G. enneantha* (*Ekman H-15498,* S), *G. cubensis* (*Ekman 9632,* S), *G. intertexta* (*Alain A-1680,* NY). —F. Denticulate to entire (left to right): *G. polymorpha* (*Pereira 8609 & Pabst 7984,* LP), *G. rotundifolia* (*Handro 157,* LP), *G. foliolosa* (*Cabrera 3451,* LP).

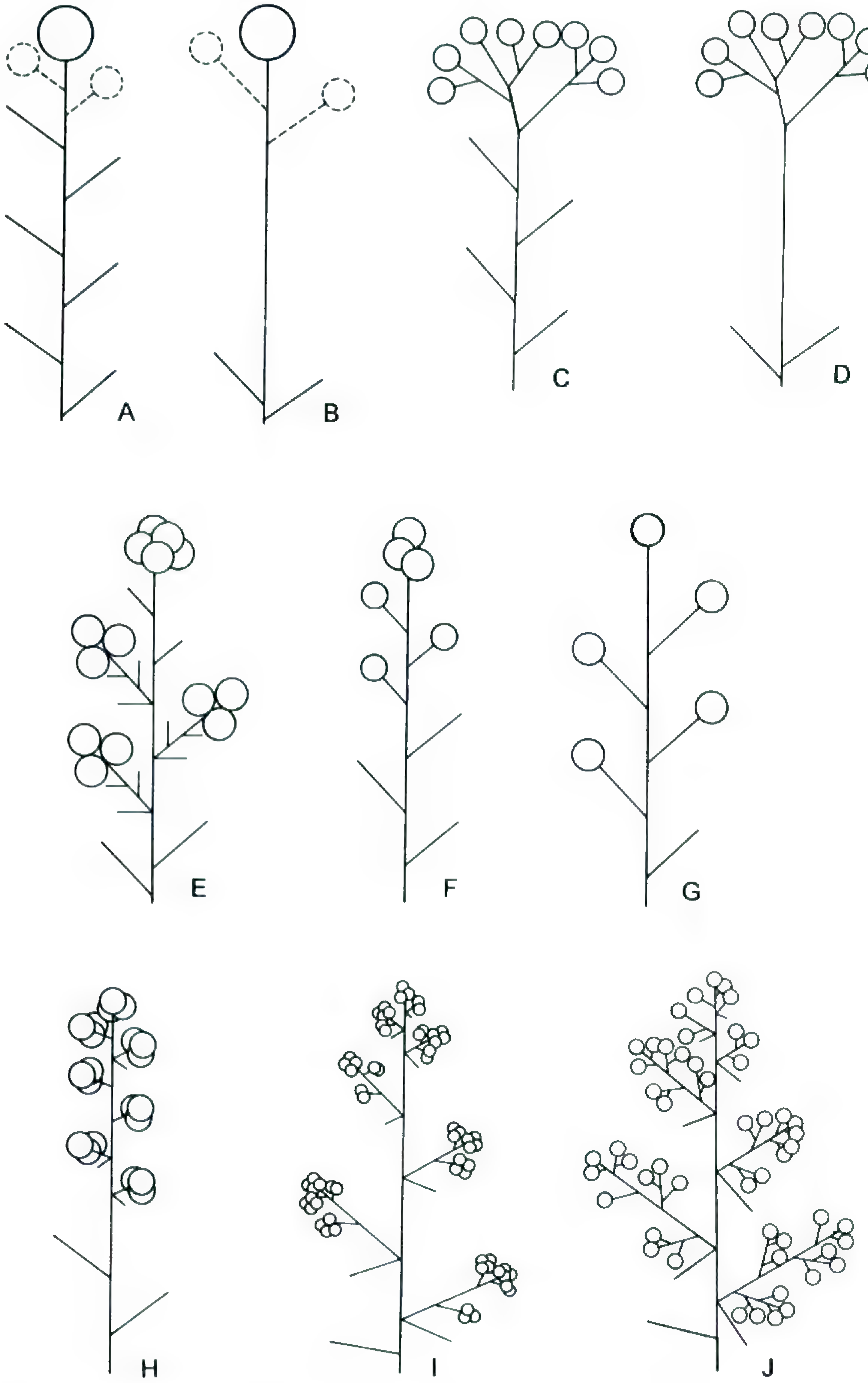

Figure 2. Types of capitulescence. —A. Solitary or few capitula short-pedunculate. —B. Solitary or few capitula long-pedunculate and scapiform. —C. Pseudocorymbs short-pedunculate. —D. Pseudocorymbs long-pedunculate and scapiform. —E. Pseudoracemes glomerulose and leafy. —F. Pseudoracemes apically glomerulose. —G. Loose pseudoracemes. —H. Pseudopanicles glomerulose. —I. Pseudopanicles short-pedunculate. —J. Loose pseudopanicles.

PALEAE

Wunderlichia is the only genus in the group with receptacular paleae. For this reason, Pruski (1991) included it in the "*Stenopadus* group." Cabrera (1971) described *Gochnatia* as typically epaleate, and only exceptionally with some paleae, but mentioned no species. However, we

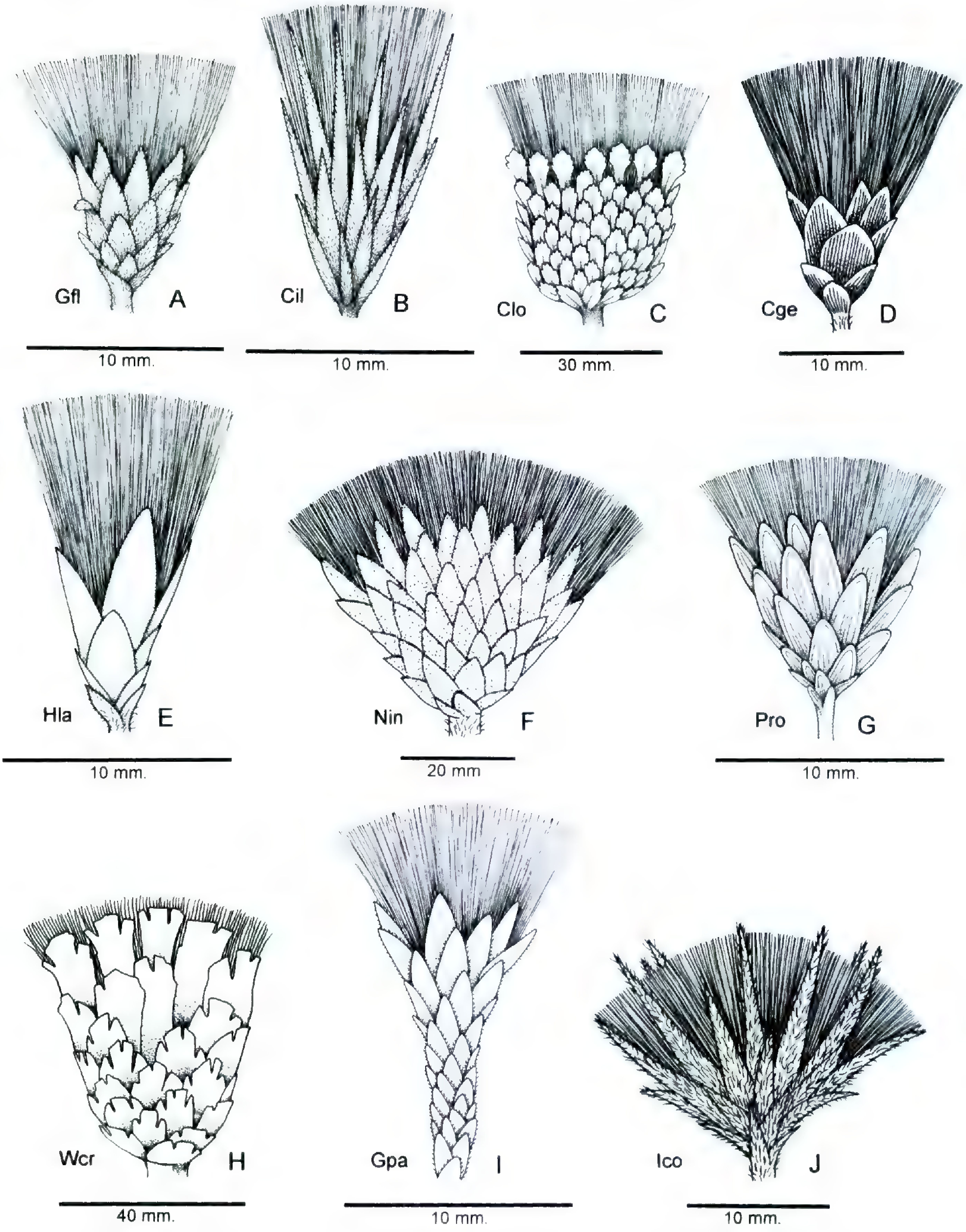

Figure 3. Involucre. A–H. Oblong to campanulate. —A. *Gochnatia floribunda* (*Hatschbach 43151*, NY). —B. *Chucoa ilicifolia* (*López Miranda 1090*, LP). —C. *Cnicothamnus lorentzii* (*Padaci 84*, LP). —D. *Cyclolepis genistoides* (*Tinto 2038*, LP). —E. *Hyalis lancifolia* (*Schinini 16098*, LP). —F. *Nouelia insignis* (*Maire 2516*, NY). —G. *Pleiotaxis rogersii* (*Rolyns 1568*, US). —H. *Wunderlichia crulsiana* (*Ratter et al. 2615*, MO). I, J. Turbinate. —I. *Gochnatia palosanto* (*Schreiter* in 1925, LP). —J. *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304*, LP).

found no evidence of paleae in any species of *Gochnatia* examined.

FLORETS

Corolla morphology and sex arrangement. Corollas in *Gochnatia* and allies may be isomorphic, subdimorphic, or clearly dimorphic. All florets of the capitula may be hermaphroditic or female (homogamous capitula), or the capitula may have central hermaphroditic florets and marginal female florets (heterogamous capitula). These features are combined as follows:

(A) Corollas isomorphic. Plants with discoid and homogamous capitula made up of hermaphroditic florets with isomorphic tubular corollas are char-

acteristic of most species of *Gochnatia* (Fig. 4A, B), *Chucoa* (Fig. 4C), *Pleiotaxis* (Fig. 4D), and *Wunderlichia* (Fig. 4E). Only *G. argyrea* of section *Moquiniastrum* has isomorphic tubulose corollas and heterogamous capitula (Sancho, 2000). Very occasionally marginal female florets (with staminodes) are found in *Chucoa* (Cabrera, 1955, and our own observations).

(B) Corollas subdimorphic. Such corollas are present only in *Gochnatia* sect. *Moquiniastrum* (except *G. argyrea* and *G. gardneri*) (Fig. 4F) and *Cyclolepis* (Fig. 4G). *Gochnatia* sect. *Moquiniastrum* includes monoecious, polygamous, and gynodioecious plants (Sancho, 2000). Polygamous and gynodioecious species have disciform capitula made up of subdimorphic corollas, i.e., central hermaphroditic florets with tubular actinomorphic corollas and coiled lobes (Fig. $4F_1$), and outer, female florets with tubular subzygomorphic corollas and erect or coiled lobes of different lengths (Fig. $4F_2$). In the gynodioecious genus *Cyclolepis* the female florets have tubular-filiform corollas (Fig. $4G_1$), and the hermaphroditic florets have tubular corollas (Fig. $4G_2$).

(C) Corollas dimorphic. Plants with radiate, homogamous capitula comprising dimorphic, hermaphroditic florets, with outer bilabiate or subbilabiate and central tubular corollas, are present in some species of *Actinoseris* (e.g., *A. polyphylla*, *A. revoluta*, *A. stenophylla*) (Fig. 4H), *Cnicothamnus* (Fig. 4I), *Hyalis* (Fig. 4J), and *Nouelia* (Fig. 4L). Plants with heterogamous capitula and the type of dimorphic corollas previously mentioned are found in *Ianthopappus* (Fig. 4K) and some species of *Actinoseris* (e.g., *A. arenaria*, *A. hatschbachii*, *A. radiata*); the outer florets are female and the central florets hermaphroditic. These truly dimorphic corollas are absent in *Gochnatia*.

It may be noted that tubular, deeply lobed corollas with coiled lobes (reaching up to 2/3 of the corolla) are present in most species of *Gochnatia* (Fig. 4A), and in *Actinoseris*, *Chucoa* (Fig. 4C), *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, and *Pleiotaxis* (Fig. 4D). Tubular, very deeply lobed corollas with straight lobes (more than ⅔ the length of the corolla, almost reaching the base) are present in most Caribbean species of *Gochnatia* sect. *Gochnatia* (e.g., *G. calcicola*, *G. cubensis*, *G. gomezii*, *G. oligantha*) (Fig. 4B). Bilabiate corollas have an external 3-dentate lip and an internal 2-cleft lip (3+2 arrangement, e.g., *Actinoseris revoluta*, *Hyalis*, *Ianthopappus*, *Nouelia*) (Fig. 4J–L), and subbilabiate corollas have an external 3-dentate and one entire, internal lip (3+1, e.g., *Actinoseris hatschbachii*, *A. polyphylla*, *Cnicothamnus*) (Fig. 4H, I).

Number of florets per capitulum. The number of florets per capitulum ranges from 4 to 300. A few species of *Gochnatia* (*G. crassifolia*, *G. magna*, *G. recurva*, *G. rotundifolia*, *G. sagraeana*) and most species of *Actinoseris*, *Cnicothamnus*, and *Wunderlichia* have 50 to 300 florets per capitulum. Some species of *Gochnatia* (e.g., *G. amplexifolia*, *G. boliviana*, *G. cordata*, *G. cowellii*, *G. patazina*, *G. vernonioides*), some species of *Actinoseris* (e.g., *A. hatschbachii*, *A. revoluta*), *Ianthopappus*, and *Nouelia* have capitula with 30 to 50 florets. Some species of *Gochnatia* (e.g., *G. arequipensis*, *G. cardenasii*, *G. ilicifolia*, *G. purpusii*), *G.* sect. *Moquiniastrum*, *Chucoa*, and *Cyclolepis* have 7 to 30 florets per capitulum, whereas some species of *Gochnatia* (e.g., *G. hypoleuca*, *G. smithii*), *G.* sects. *Leucomeris* and *Pentaphorus*, a few Caribbean species of *G.* sect. *Gochnatia* (e.g., *G. calcicola*, *G. cubensis*, *G. gomezii*, *G. oligantha*), and *Hyalis* have capitula with 4 to 6 florets.

Corolla color. The corollas in *Gochnatia* are predominantly yellow or cream. In some species (e.g., *G. rotundifolia*, *G. decora*, *G. spectabilis*, *G. foliolosa*) they are white and/or lilac. In others (e.g., *G. cowellii*, *G. ilicifolia*, *G. intertexta*, *G. mantuensis*, *G. sagraeana*) they are orange. The corollas are white, pink, or purple in *Actinoseris*; in *Cnicothamnus* they are orange; in *Chucoa* and *Cyclolepis*, yellow; in *Hyalis* lilac; in *Nouelia* white; in *Pleiotaxis* deep red, pink, white, or cream; in *Wunderlichia* white or yellow. *Ianthopappus* shows white marginal corollas and purple disc corollas.

ANTHERS

As well as most species of the tribe Mutisieae, all the taxa in this study have an apical anther appendage and basal tails. The apical appendage can be viewed as an adaptation to protect the pollen in the anther tube from moisture and insect predators until the stigma and style push upward through it for pollen presentation (Stuessy et al., 1996).

With the exception of *Chucoa*, with acute anther appendages (Fig. 5A), anther appendages in *Gochnatia* and related taxa have usually been described as apiculate. *Pleiotaxis* differs in its thickened and bulbous apical appendage (Fig. 5B).

Analysis of this feature in all the genera under study revealed further variation in its shape that is particularly useful in grouping species within *Gochnatia*. The appendage can be short (anthers

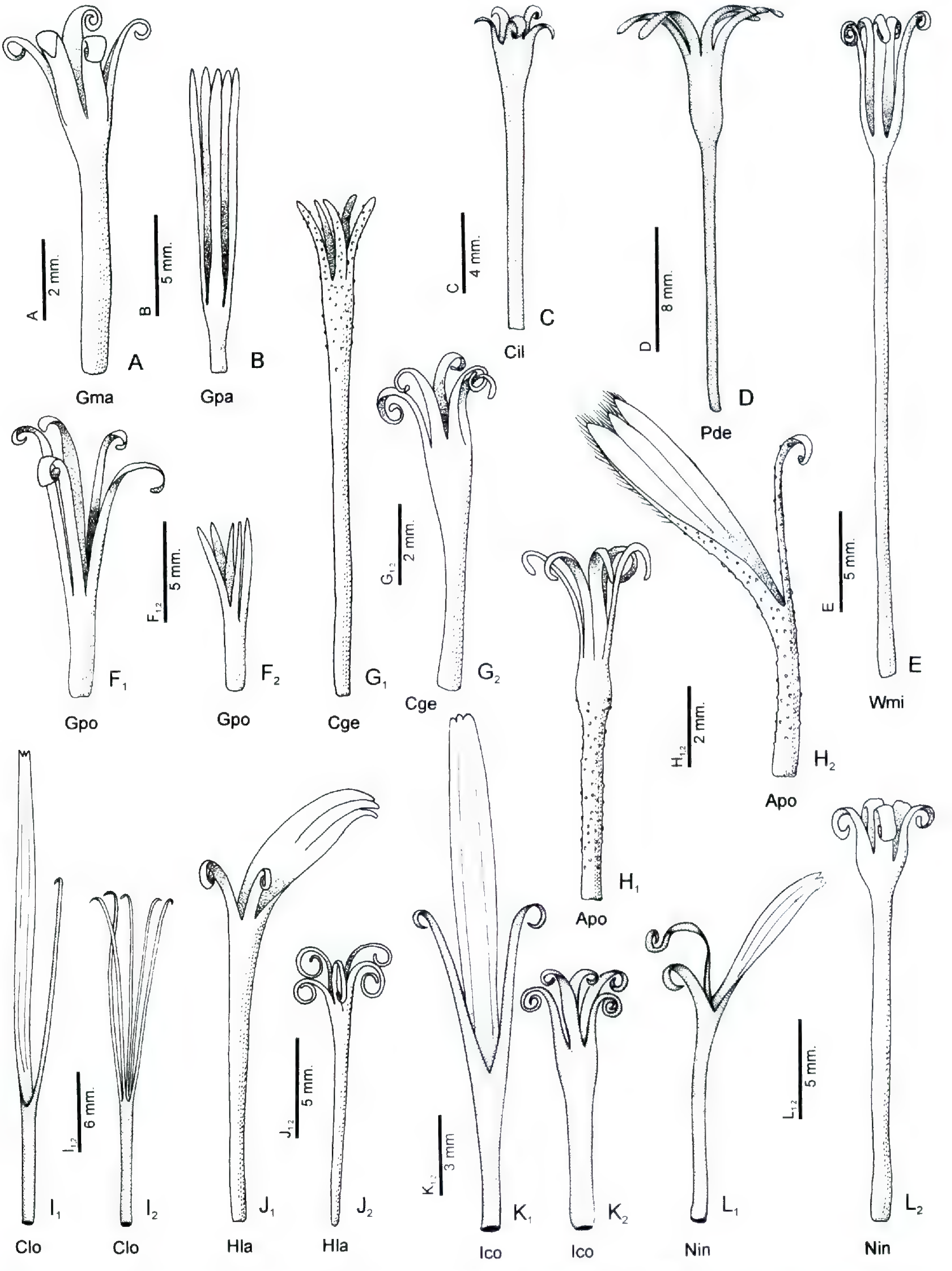

Figure 4. A–E. Isomorphic corolla. —A. *Gochnatia magna* (*Cronquist 11277*, NY). —B. *G. paucifloscullosa* (*Eggers 3866*, K). —C. *Chucoa ilicifolia* (*López Miranda 1090*, LP). —D. *Pleiotaxis dewevrei* (*de Hitte 288*, US). —E. *Wunderlichia mirabilis* (*Martinelli & Stutts 999*, NY). F, G. Subdimorphic corolla. —F. *Gochnatia polymorpha* (*Hashimoto 624*, LP): F_1, disc corolla, F_2, marginal corolla. —G. *Cyclolepis genistoides* (*Cabrera 3782*, LP): G_1, marginal corolla, G_2, disc corolla. H–L. Dimorphic corolla. —H. *Actinoseris polyphylla* (*Hatschbach 35304*, LP): H_1, disc corolla, H_2, marginal corolla. —I. *Cnicothamnus lorentzii* (*Cabrera et al. 22576*, LP): I_1, marginal corolla, I_2, disc corolla. —J. *Hyalis lancifolia* (*Schinini 16098*, LP): J_1, marginal corolla, J_2, disc corolla. —K. *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304*, LP): K_1, marginal corolla, K_2, disc corolla. —L. *Nouelia insignis* (*Maire 2516*, NY): L_1, marginal corolla, L_2, disc corolla.

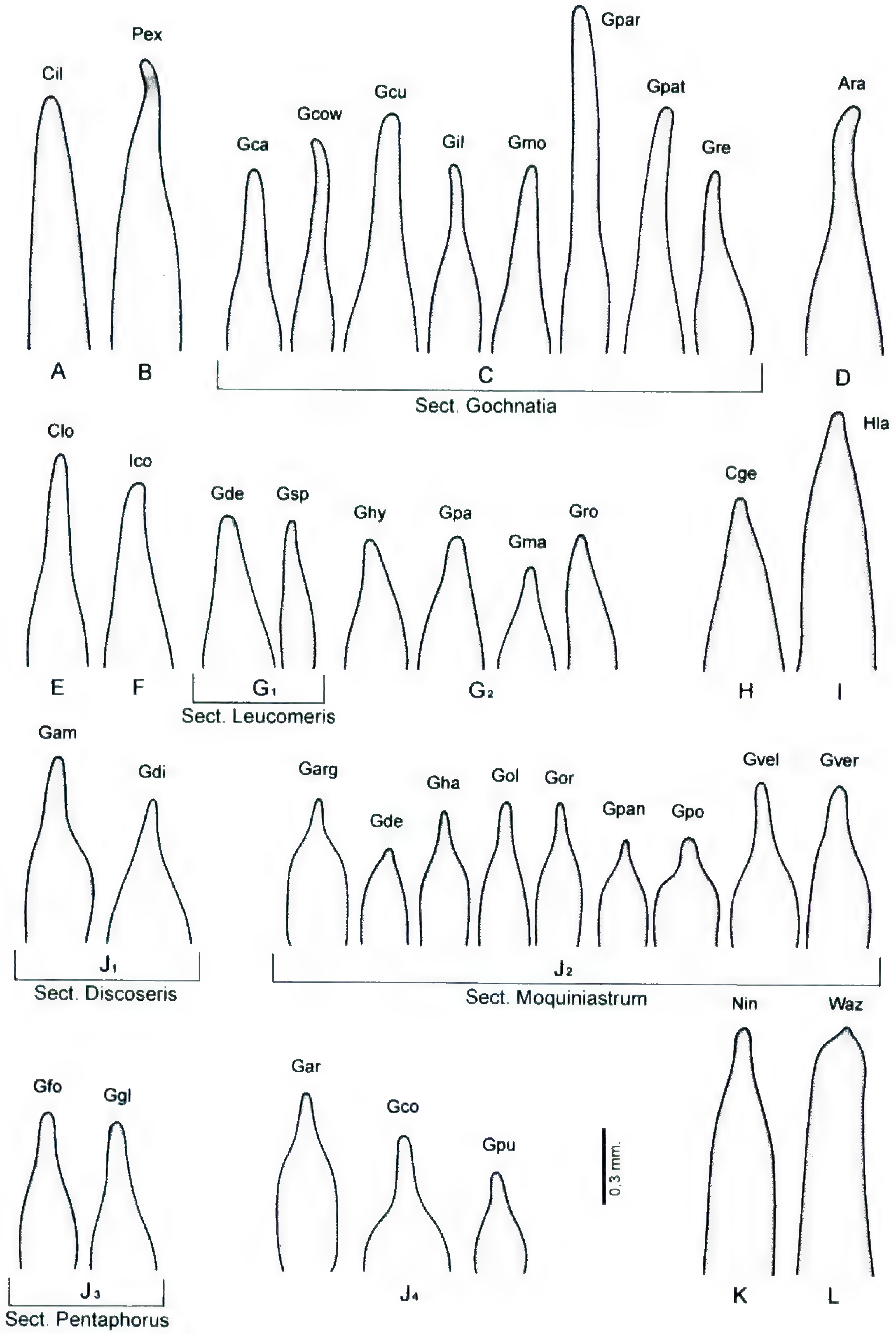

Figure 5. Apical anther appendage. —A. Not apiculate: *Chucoa ilicifolia* (*López Miranda 1090*, LP). —B. Apiculate bulbous: *Pleiotaxis eximia* (*Rolyns 1836*, US). C–F. Caudate anther appendage. —C. *Gochnatia* sect. *Gochnatia* sensu Cabrera (from left to right): *Gochnatia cardenasii* (*Cordo & Ferrer 88-B-17*, SI), *G. cowellii* (*Britton & Cowell 10183*, NY), *G. curviflora* (*Jeréz et al. 49120*, LP), *G. ilicifolia* (*Small & Carter 8526*, K), *G. montana* (*Ekman 18725*, S), *G. parvifolia* (*Shafer 2938*, NY), *G. patazina* (*López & Sagástegui 3409*, LP), *G. recurva* (*León 20946*, LP). —D. *Actinoseris*

apiculate) to very long (anthers apically caudate). In addition, it can abruptly terminate in a sharp point, or gradually taper above into an attenuate point. The following three combinations were observed:

(1) Apically caudate (Fig. 5C–E): in most species of *Gochnatia* sect. *Gochnatia* (except *G. boliviana, G. buchii, G. microcephala, G. tortuensis,* and *G. vernonioides* with abruptly apiculate apices) (Fig. 5C), *Actinoseris* (Fig. 5D), and *Cnicothamnus* (Fig. 5E).

(2) Attenuate apiculate (Fig. 5G): in *Gochnatia* sect. *Leucomeris, G. hypoleuca, G. palosanto, G. magna,* and *G. rotundifolia.*

(3) Abruptly apiculate (Fig. 5J–L): in *Gochnatia* sect. *Discoseris,* sect. *Moquiniastrum* (short appendage in *G. argentina, G. densicephala,* and *G. floribunda*), and sect. *Pentaphorus, Gochnatia arborescens, G. cordata, G. purpusii* (Fig. 5J), *Nouelia* (Fig. 5K), and *Wunderlichia* (very short) (Fig. 5L).

Although useful in distinguishing taxa, some overlap exists between these broad categories such as between apically caudate-attenuate (e.g., *Ianthopappus,* Fig. 5F), attenuate-abruptly apiculate (e.g., *Cyclolepis,* Fig. 5H; *Hyalis,* Fig. 5I), and abruptly apiculate-caudate (e.g., *G. velutina,* Fig. 5J).

Anther tails are free and can be smooth or laciniate. They are smooth in the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. attenuata, G. ilicifolia,* and *G. microcephala*), some species of *Gochnatia* sect. *Moquiniastrum* (e.g., *G. barrosii, G. densicephala, G. floribunda, G. paniculata*), some species of *Gochnatia* sect. *Hedraiophyllum* (e.g., *G. arborescens, G. magna, G. purpusii*), *Chucoa, Cnicothamnus,* and *Wunderlichia.* The tails are laciniate, at least in one side, in most species of *Gochnatia* (e.g., *G.* sect. *Discoseris, G.* sect. *Leucomeris,* the South American species of *G.* sect. *Gochnatia,* and *G. glutinosa*), and in *Actinoseris, Cyclolepis, Hyalis, Ianthopappus, Nouelia,* and *Pleiotaxis.*

STYLE

Most taxa have smooth styles except for *Wunderlichia* (Fig. 6A) and *Chucoa* (Fig. 6B) with dorsally papillose styles, i.e., with the two branches (rounded and acute at the apex, respectively) covered by short sweeping hairs, and *Pleiotaxis* (Fig. 6C) with a subapical crown of short hairs. All species of *Gochnatia* (Fig. 6D, E), *Actinoseris* (Fig. 6F), *Cnicothamnus* (Fig. 6G), *Cyclolepis* (Fig. 6H), *Hyalis* (Fig. 6I), *Ianthopappus* (Fig. 6J), and *Nouelia* (Fig. 6K) have smooth, apically rounded styles. Most have the inner surface of the branches covered by stigmatic papillae prolonged into the outer surface of the style constituting a ridge of cells, which is less evident in *Cnicothamnus.*

TRICHOMES

Leaf pubescence. Excluding some species such as *Gochnatia rotundifolia, Actinoseris hatschbachii, A. stenophylla,* and *Hyalis lancifolia,* which have glabrous leaves, at least when mature, there are five different types of trichomes in *Gochnatia* and its relatives.

(1) Oblique septate flagellate hairs: one or two foot cells, one- or more-celled stalks or stipes, and unicellular, very long, flagellate, tubular heads (Fig. 7A). This trichome type is present in most species of *Gochnatia, Chucoa, Cnicothamnus, Pleiotaxis,* and *Wunderlichia.*

(2) Two-armed hairs (or T-shaped, malpighiaceous, anvil, dolabriform hairs): one or two foot cells, uniseriate, generally two- to more-celled stalks, and unicellular heads. The apical cell, which constitutes the head, initially assumes the shape of a hammer and later becomes T-shaped by further outgrowth of the two ends (Fig. 7B, C). This trichome type is present in *Gochnatia* sect. *Moquiniastrum* (Fig. 7B) and *G. cordata, Cyclolepis* (Fig.

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radiata (*Hatschbach 690,* LP). —E. *Cnicothamnus lorentzii* (*Ruiz Leal 14162,* LP). —F. *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304,* LP). —G–I. Attenuate-apiculate anther appendage. G_1, *Gochnatia* sect. *Leucomeris* sensu Cabrera (from left to right): *Gochnatia decora* (*Maung Mya 5309,* LP), *G. spectabilis* (*Galrola 32,* LP). G_2, *G. hypoleuca* (*González Quintero 3215,* LP), *G. palosanto* (*Schreiter* in 1925, LP), *G. magna* (*Fernández 3666,* NY), *G. rotundifolia* (*Joly 596,* LP). —H. *Cyclolepis genistoides* (*Correa 3172 & Nicora,* LP). —I. *Hyalis lancifolia* (*Cabrera 4083,* LP). —J–L. Abruptly apiculate anther appendage. J_1, *Gochnatia* sect. *Discoseris* sensu Cabrera (from left to right): *Gochnatia amplexifolia* (*Hatschbach 35312,* LP), *G. discoidea* (*Blanchet 3345,* LP). J_2, *Gochnatia* sect. *Moquiniastrum* sensu Cabrera (from left to right): *G. argyrea* (*Hatschbach 9578,* LP), *G. densicephala* (*Sheperd 5771 et al.,* UEC), *G. haumaniana* (Rojas, herb. *Hassler 9752,* LP), *G. oligocephala* (*Blanchet 3288,* US), *G. orbiculata* (*Brade 5523,* US), *G. paniculata* (*Gardner 4810,* US), *G. polymorpha* (*Glaziou* in 1876, LP), *G. velutina* (*Smith & Klein 14885,* LP), *G. vernonioides* (*López et al. 4364,* LP). J_3, *Gochnatia* sect. *Pentaphorus* sensu Cabrera (from left to right): *G. foliolosa* (*Cabrera 3451,* LP), *G. glutinosa* (*King 183,* LP). J_4 (from left to right): *G. arborescens* (*Johnston 4023,* LP), *G. cordata* (*Rambo 545,* LP), *G. purpusii* (*Purpus 4248,* NY). —K. *Nouelia insignis* (*Maire 2516,* NY). —L. *Wunderlichia azulensis* (*Harley et al. 25209,* MO) (very shortly apiculate).

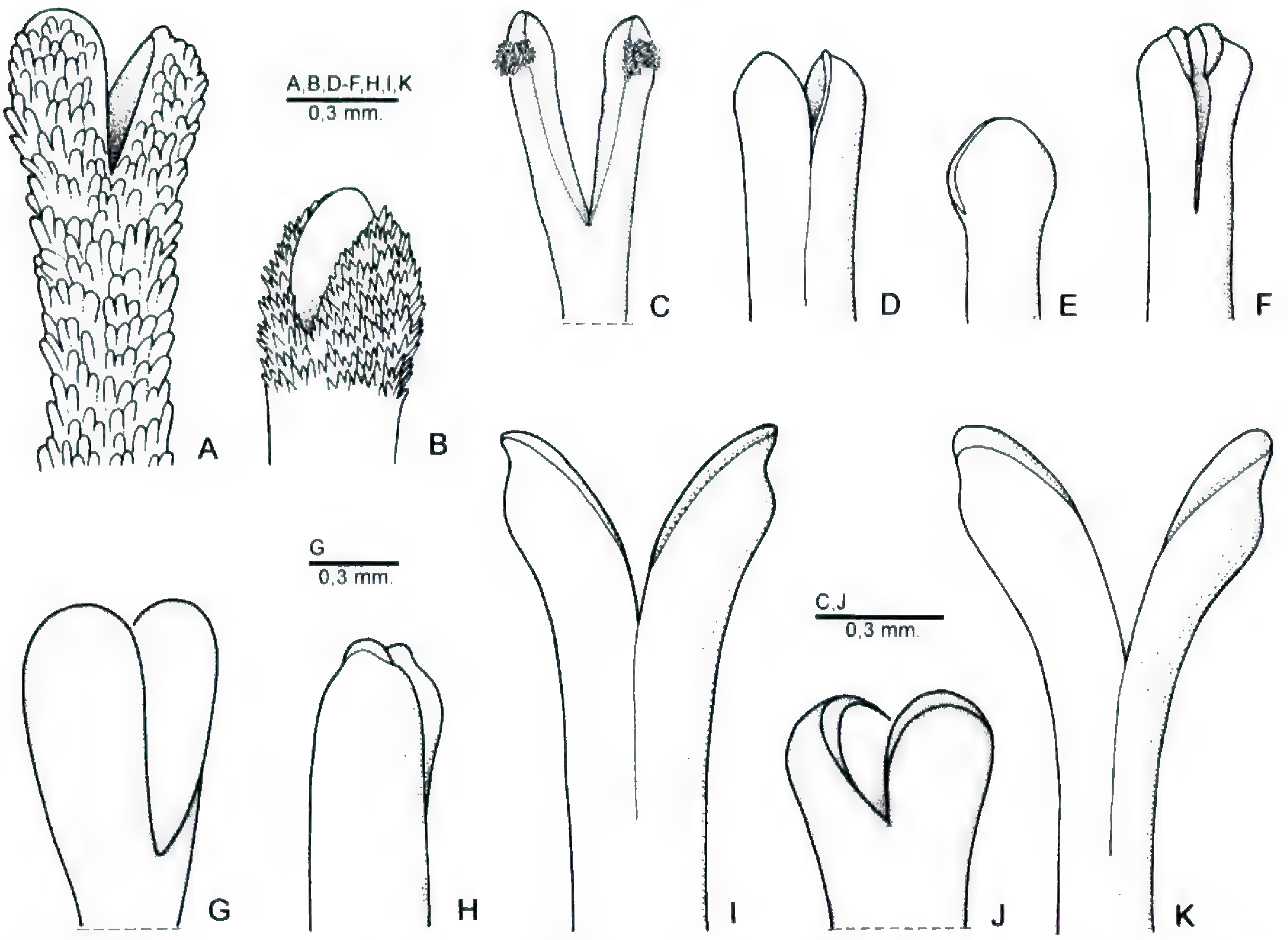

Figure 6. Style branches. A–C. Papillose style branches. —A. *Wunderlichia azulensis* (*Harley et al. 25209*, MO). —B. *Chucoa ilicifolia* (*López Miranda 1090*, LP). —C. *Pleiotaxis eximia* (*Rolyns 1836*, US). D–K. Smooth style branches. —D. *Gochnatia discoidea* (*Blanchet 3345*, LP). —E. *G. cordata* (*Rambo 545*, LP). —F. *Actinoseris angustifolia* (*Hatschbach 28756*, LP). —G. *Cnicothamnus lorentzii* (*Ruiz Leal 14162*, LP). —H. *Cyclolepis genistioides* (*Zardini & Kiesling 114*, LP). —I. *Hyalis argentea* (*Ruiz Leal 3701*, LP). —J. *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304*, LP). —K. *Nouelia insignis* (*Maire 2516*, NY).

7C), and *Hyalis argentea*. In *Nouelia* one end of the apical cell is very short.

(3) Three- to 5-armed hairs (or 3- to 5-branched, stellate hairs sensu Cabrera, 1971): similar to the 2-armed hairs, but the apical cell has 3 to 5 branches (Fig. 7D). The apical cell does not divide and thus the head remains one-celled. This type is found only in *Gochnatia barrosii* and *G. rusbyana* of section *Moquiniastrum*.

(4) Multistoried T-shaped hairs: similar to the 2-armed hairs, but further periclinal divisions take place in the apical cell. The head is thus comprised of 3 or 4 one-celled layers, all oriented transversally and parallel, but of different lengths (Fig. 7E). This type of trichome, not very common in Asteraceae, has been reported in the tribe Senecioneae (Robinson, 1989). *Ianthopappus* is the only genus with this type of trichome.

(5) Biseriate glandular hairs: comprised of 2 rows of cells in the body, with two to many cells in each row, enclosed by a persistent or collapsed cuticular vesicle (Fig. 7F, G). Glandular hairs are widespread in all the taxa studied, and especially in species of *Gochnatia* sect. *Pentaphorus* (i.e., *Gochnatia foliolosa*, *G. glutinosa*) where they cover almost the entire surface of the leaf, with the flagellate hairs restricted to the margins.

Achenial pubescence. Glabrous or slightly papillose achenes occur in *Chucoa*, in a few species of *Pleiotaxis* (e.g., *P. decipiens*, *P. huillensis*, *P. linearifolia*, *P. welwitschii*), and *Wunderlichia* (e.g., *W. bahiensis*, *W. crulsiana*, *W. insignis*, *W. senaei*). The remaining taxa have villose achenes. Three types of achenial trichomes were found: Duplex or twin hairs, leaf-like hairs (2-armed, oblique-septate flagellate), and glandular hairs.

(1) Duplex or twin hairs: Twin hairs are the common type in Asteraceae, comprised of two triangular or rectangular basal cells, one sometimes reduced, and two cylindrical or elliptical hair cells, equal or subequal in length, generally in contact up to their tips (Hess, 1938; Freire & Katinas, 1995) (Fig. 7H, I). All the taxa studied, in-

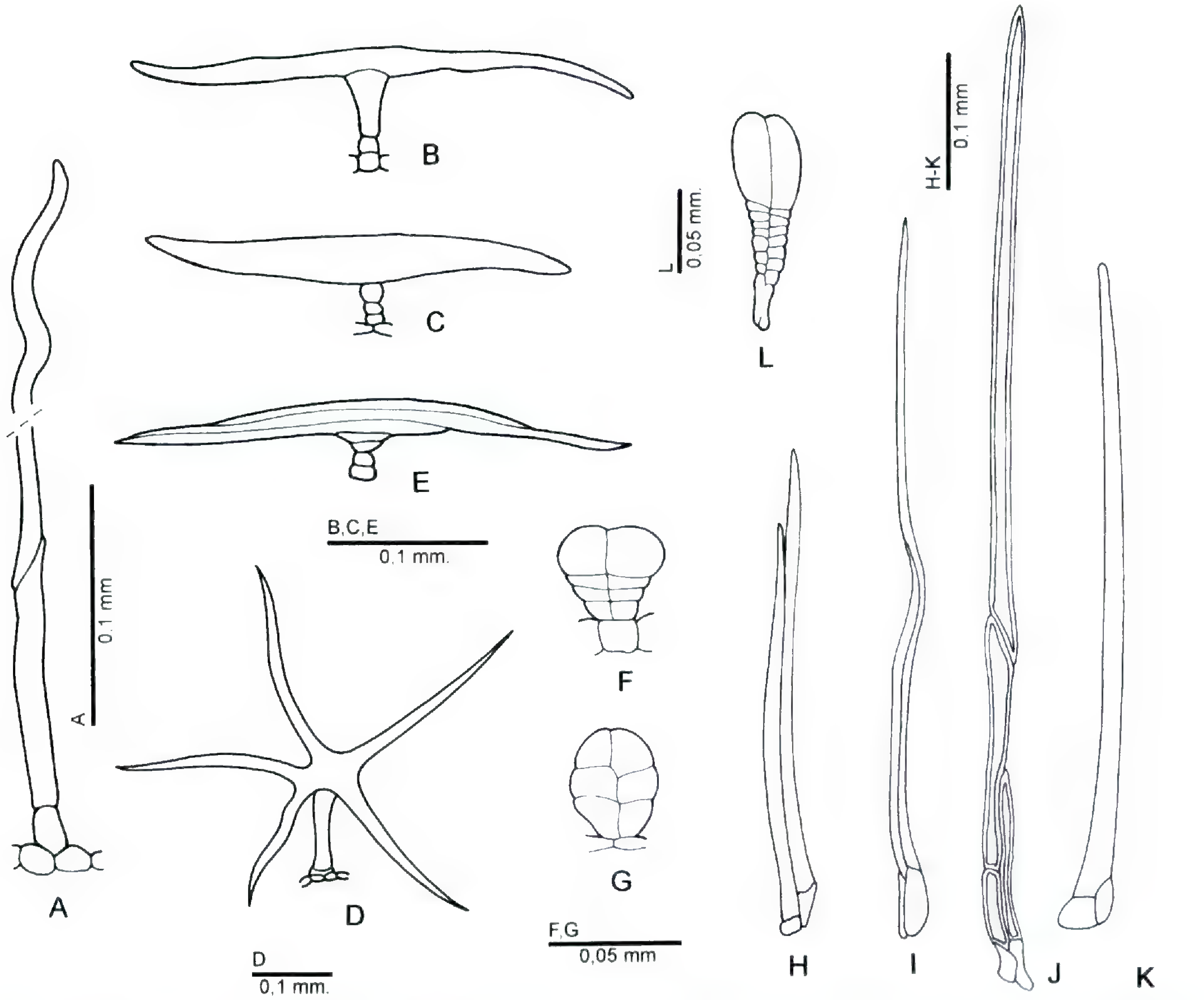

Figure 7. Trichomes. A–G. Leaf hairs. —A. Oblique septate flagellate hair: *Gochnatia tortuensis* (*Ekman H-3553*, S). B, C. 2-armed hair. —B. *Gochnatia polymorpha* (*Pedersen 8587*, LP). —C. *Cyclolepis genistoides* (*Correa 3172 & Nicora*, LP). —D. 3- to 5-armed hair: *Gochnatia barrosii* (*Hatschbach 16945*, LP). —E. Multistoried T-shaped hair: *Ianthopappus corymbosus* (*Palacios & Cuezzo 2304*, LP). F, G. Biseriate glandular hairs. —F. *Gochnatia discoidea* (*Blanchet 3345*, LP). —G. *Gochnatia glutinosa* (*Fabris 1343*, LP). H–L. Achenial hairs. H–K. Duplex hairs: *Wunderlichia azulensis* (*Harley et al. 25209*, MO). H–I. Duplex hairs with one of the hair cells shorter. —J. Septate duplex hair. —K. Duplex hair with only one hair cell. —L. Capitate glandular biseriate hair: *Gochnatia cowellii* (*Britton & Cowell 10183*, NY).

cluding most species of *Gochnatia*, have achenes with twin hairs, usually very long and filiform. In some cases twin hairs have one hair cell very short (e.g., *Gochnatia purpusii*, *G. recurva*, *G. tortuensis*, *Cyclolepis*, *Wunderlichia azulensis*, *W. mirabilis*) (Fig. 7I), they are septate (e.g., *Gochnatia hatschbachii*, *G. oligocephala*, *Hyalis*, *Pleiotaxis eximia*, *Wunderlichia azulensis*, *W. mirabilis*) (Fig. 7J), or have only one hair cell (*Wunderlichia azulensis*) (Fig. 7K).

(2) Leaf-like hairs: Two-armed hairs in the achenes similar in morphology to the leaf hairs, as described above, were found in *Gochnatia orbiculata*. Only a few species of *Gochnatia* (e.g., *G. cubensis*, *G. magna*, *G. ramboi*) have oblique-septate flagellate hairs.

(3) Achenial biseriate glandular hairs: These are similar to those on the leaves (Fig. 7F, G) and are very widespread in the group under study, occurring with the other types. A modification of the typical biseriate glandular hair with a very enlarged head, i.e., capitate glandular hair (Metcalfe & Chalk, 1950) (Fig. 7L), was found in the Caribbean species of *Gochnatia* sect. *Gochnatia*.

PAPPUS

In all taxa analyzed the pappus is comprised of rigid and scabrid bristles. However, there is interesting variation in bristle length and width, modifications of the lateral cells at the apex of the bristles, and in the number of series of the bristles. Five pappus types were found.

Type A. All the bristles have the same length

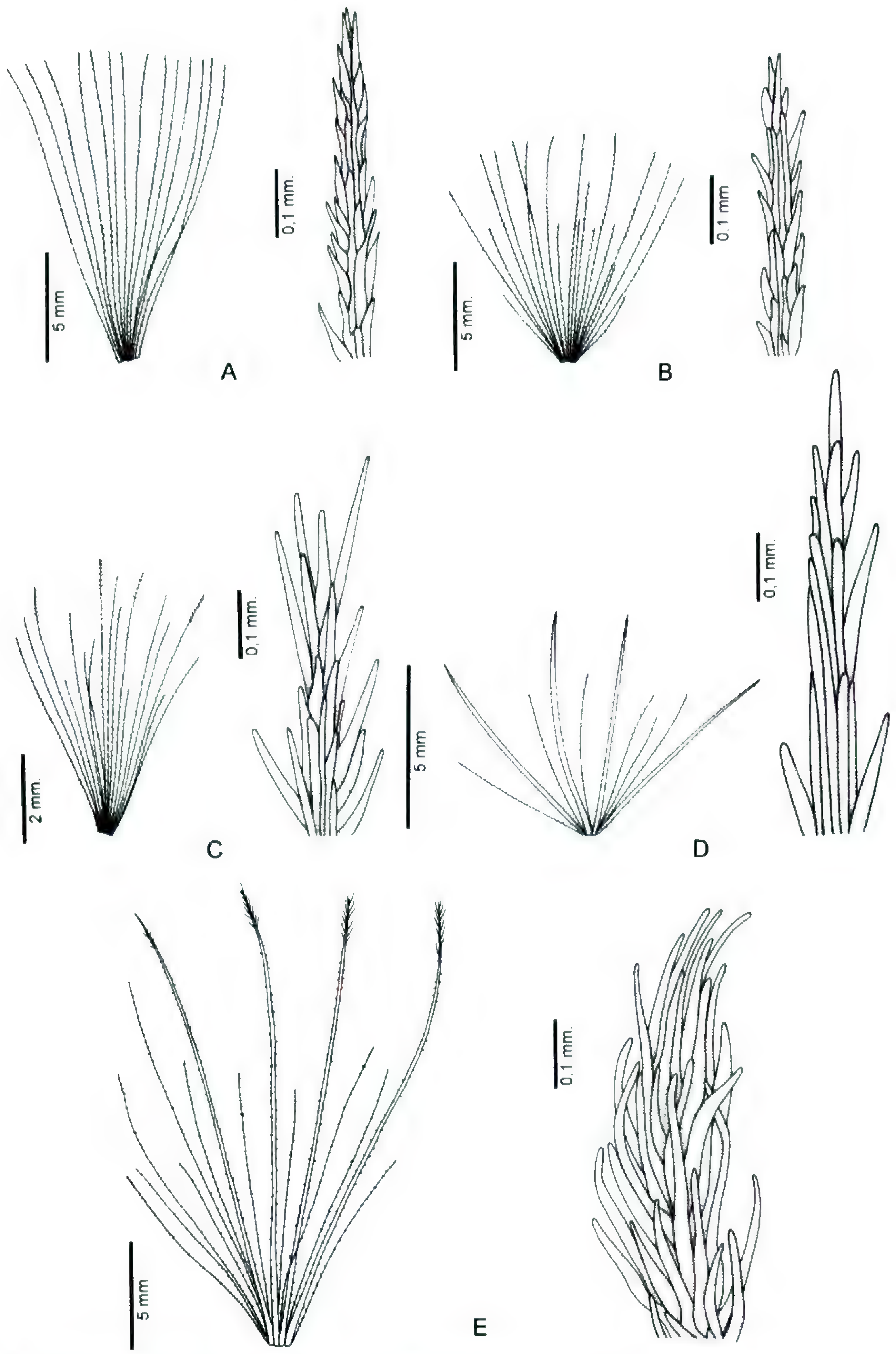

Figure 8. Pappus. General aspect (on the left) and detail of bristle apex (on the right). —A. Type A: *Gochnatia recurva* (*León 20946*, LP). —B. Type B: *Gochnatia decora* (*Maung Mya 5309*, LP). —C. Type C: *Gochnatia cordata* (*Serrano 6*, LP). —D. Type D: *Gochnatia glutinosa* (*Fabris 1343*, LP). —E. Type E: *Wunderlichia mirabilis* (*Irwin et al. 9913*, NY).

and width (Fig. 8A). This is present in the Caribbean species of *Gochnatia* sect. *Gochnatia* (except *G. cubensis*, *G. oligantha*, *G. sagraeana*, *G. tortuensis*), *G.* sect. *Discoseris*, and *Actinoseris*.

Type B. All the bristles have the same width, but about half are shorter than the others (Fig. 8B). This type is present in *Gochnatia* sect. *Leucomeris*, the South American species of section *Gochnatia*,

most species of section *Hedraiophyllum*, and *Chucoa*, *Hyalis*, and *Nouelia*.

Type C. All the bristles have the same width, half of them are shorter, and the longest are plumose at the apex (Fig. 8C). This pappus is present in *Gochnatia cordata*, *G.* sect. *Moquiniastrum*, and *Ianthopappus*.

Type D. Half of the bristles are long and relatively wide and flat (somewhat paleaceous) and the other half are short and thin (Fig. 8D). This type is present in *Gochnatia* sect. *Pentaphorus* and some species of *Pleiotaxis* (e.g., *P. dewevrei*, *P. eximia*, *P. pulcherrima*), all with the long bristles acute at the apex, and in *Cnicothamnus*, which has the long bristles clavate at the apex.

Type E. Half of the bristles are long and relatively wide and flat (somewhat paleaceous) and half are short and thin; all are scabrid, but the longer are plumose at the apex (Fig. 8E). This kind of pappus is found in *Cyclolepis*, some species of *Pleiotaxis* (e.g., *P. huillersii*, *P. rogersii*), and *Wunderlichia*.

The type A pappus, i.e., with all the bristles of the same length, is 1-seriate with 30 to 40 bristles. Types B–E, i.e., with the bristles of different length, are 2- to 3-seriate with more than 50 bristles.

Discussion

Character Value

Some characters such as habit, most leaf features, and pappus vary within *Gochnatia*. Other characters, although constant and common to all species of *Gochnatia*, are not exclusive to it, such as multiseriate involucres, tailed anthers with apiculate anther appendages, and smooth style branches. Table 2 shows this and the main morphological characters that allow the genera associated with *Gochnatia* to be distinguished. Some of the characters studied merit a brief discussion.

The involucre of *Gochnatia*, resembling a spruce cone, suggested by Hansen (1991) as a distinguishing character for the group of *Gochnatia* and its associated genera, also occurs in other Mutisieae such as *Aphyllocladus*, *Dinoseris*, *Hyaloseris*, and *Stenopadus*, which are not very closely related to *Gochnatia*. We do not therefore consider that this feature has diagnostic value.

Corolla morphology has been used as a key diagnostic character in Mutisieae. The tubular actinomorphic (Fig. 4A–E), tubular-filiform (Fig. $4G_1$), tubular subzygomorphic (Fig. $4F_2$), subbilabiate (Fig. $4H_2$, I_1), and bilabiate corollas (Fig. $4J_1$, K_1, L_1) present in the taxa studied show the great variation of this character in Mutisieae. Cabrera (1961, 1977) characterized Gochnatiinae and Barnadesiinae (the latter subtribe currently constitutes the subfamily Barnadesioideae; Bremer & Jansen, 1992) in the first comprehensive key to subtribes of Mutisieae by having more or less actinomorphic, deeply 5-lobed disc corollas, with equal or unequal segments, but never truly bilabiate, and bilabiate or subligulate ray corollas. The Mutisiinae and Nassauviinae, on the other hand, have clearly bilabiate (the disc florets exceptionally actinomorphic) or ligulate disc and ray florets. According to this key all the taxa studied, although variable in their corollas, would correspond to the subtribe Gochnatiinae (sensu Cabrera, 1977). Other authors (e.g., Robinson, 1991; Bremer, 1994) regard the distinction between Gochnatiinae and Mutisiinae, based only on the actinomorphic versus bilabiate disc florets, to be artificial and recognize only Mutisiinae sensu lato.

Apiculate anther appendages have been strongly considered to be an advanced character within Mutisieae (Cabrera, 1977; Hansen, 1991; Karis et al., 1992; Bremer, 1994). The shape of the anther appendage, i.e., caudate, attenuate, and abruptly apiculate (Fig. 5C–L), led to distinction within *Gochnatia* and also among genera. Indeed, *Gochnatia* can be associated with *Actinoseris*, *Cnicothamnus*, *Cyclolepis*, *Hyalis*, *Ianthopappus*, *Nouelia*, and *Wunderlichia* by the common possession of flat (not bulbous), apiculate anther appendages. *Chucoa* and *Pleiotaxis* (Fig. 5A, B), based on their acute and bulbous anther appendages, respectively, are very different. The current tribal position of *Pleiotaxis* is controversial. Some authors regard *Pleiotaxis* as forming part of a mutisiean "*Dicoma*-group" (Bremer, 1994; Ortiz, 2000; Ortiz & Coutinho, 2001). According to Hansen (1991), this group of genera (including *Pleiotaxis*) should be excluded from Mutisieae by features of style branches, anthers, and pollen type.

Smooth styles are revealed as another informative feature in this group of taxa, although the value of this character is controversial. Some authors (Bremer, 1987) consider the glabrous styles to be plesiomorphic within Asteraceae (although the Lobeliaceae, characterized by hairy style branches, were used as an outgroup), while others (Stuessy et al., 1996) postulate the smooth condition to be derived with Calyceraceae as the outgroup. At present the hypothesis that Calyceraceae are the sister group of Asteraceae (e.g., Albach et al., 2001; Urtubey & Stuessy, 2001) is widely accepted. Since the style branches in Calyceraceae are papillose

Table 2. Main morphological characters that allow the distinction of *Gochnatia* and associated genera. The exclusive characters are in boldface. Uncommon features are in parentheses. Characters that distinguish *Gochnatia* from other genera are in *italics*.

	Gochnatia	*Actinoseris*	*Chucoa*	*Cnicothamnus*	*Cyclolepis*	*Hyalis*	*Ianthopappus*	*Nouelia*	*Pleiotaxis*	*Wunderlichia*
Habit	trees, shrubs, (subshrubs)	herbs	shrubs	trees	**spinose, aphyllous** shrubs	subshrubs	subshrubs	shrubs	herbs	trees
Non-glandular foliar trichomes	flagellate, 2-armed, **3- to 5-armed**	flagellate	flagellate	flagellate	2-armed	2-armed	**multistoried T-shaped**	2-armed	flagellate	flagellate
Receptacle	epaleate	epaleate	epaleate	epaleate	epaleate	epaleate	epaleate	epaleate	epaleate	**paleate**
Capitula	*homogamous* (heterogamous)	homogamous, heterogamous	homogamous (heterogamous)	homogamous	homogamous	homogamous	heterogamous	homogamous	homogamous	homogamous
Phyllaries apical appendage	absent	absent	absent	**rhombic, lacerate**	absent	absent	absent	absent	absent	absent
Corollas	*isomorphic* (subdimorphic)	dimorphic	isomorphic	dimorphic	subdimorphic	dimorphic	dimorphic	dimorphic	isomorphic	isomorphic
Corolla color	yellow, cream (lilac, orange, white)	white, pink, purple	yellow	orange	yellow	lilac	white and purple	white	red, pink, white, cream	white, yellow
Anther apical appendage	*apiculate*: abruptly, caudate, attenuate	apiculate: caudate	**acute**	apiculate: caudate	apiculate: abruptly-attenuate	apiculate: abruptly-attenuate	apiculate: caudate-attenuate	apiculate: abruptly	apiculate: **thickened, bulbose**	apiculate: abruptly
Anther tails	smooth, laciniate	laciniate	smooth	smooth	laciniate	laciniate	laciniate	laciniate	laciniate	smooth
Style branches	*smooth*	smooth	**pubescent: dorsally**	smooth	smooth	smooth	smooth	smooth	**pubescent: subapically**	**pubescent: dorsally**
Pappus	Types A, B, C, D	Type A	Type B	Type D	Type E	Type B	Type C	Type B	Types D, E	Type E

(Hansen, 1992, and our own observations) the smooth style branches in Asteraceae become an advanced character for the family.

The multistoried T-shaped hair (Fig. 7E), the 2-, and 3- to 5-armed hairs (Fig. 7B–D), the capitate glandular achenial hair (Fig. 7L), and the pappus types established here (Fig. 8) are revealed as new diagnostic characters. In fact: (1) the multistoried T-shaped hair is exclusive to *Ianthopappus* and becomes another character to distinguish it; (2) the 2-armed hairs are present in *Gochnatia cordata*, *G.* sect. *Moquiniastrum*, *Cyclolepis*, *Hyalis*, and *Nouelia*; (3) the 3- to 5-armed hairs are exclusive to some species of *Gochnatia* sect. *Moquiniastrum*; (4) the capitate glandular achenial hairs, with a very enlarged head, distinguish most of the Caribbean species of *Gochnatia* sect. *Gochnatia*; and (5) pappus types A, B, C, D are present in *Gochnatia* and allow the distinction of sections within the genus (see below), while type E is present only in *Cyclolepis*, *Pleiotaxis*, and *Wunderlichia*.

Circumscription of *Gochnatia* and Its Sections

Our morphological analysis confirms that *Gochnatia* has no single exclusive feature that distinguishes it from related taxa, but it can be defined by a set of characters, i.e., homogamous (rarely heterogamous) capitula, isomorphic (tubular) to subdimorphic (tubular and tubular subzygomorphic) corollas, apiculate anther appendages, and smooth style branches (Table 2).

After analyzing the morphological features of *Gochnatia*, the sections established by Cabrera (1971) were reviewed and some changes are proposed.

The distinctiveness of two of the six Cabrera sections, sect. *Discoseris* and sect. *Pentaphorus*, was confirmed and additional characters supporting them were found. For instance, *Discoseris* has pappus type A and *Pentaphorus* type D.

Gochnatia cordata, placed by Cabrera in section *Hedraiophyllum*, has characters that link it to section *Moquiniastrum* such as the 2-armed foliar hairs (Fig. 7B), numerous capitula arranged in glomerulose pseudopanicles (Fig. 2H), and pappus type C (Fig. 8C) and must be included in this section. However, it constitutes the type species of section *Hedraiophyllum* established by Lessing (as a subgenus) in 1832 and has priority over the name of section *Moquiniastrum* established by Cabrera in 1971 (with *G. polymorpha* as the type species). Thus, the name *Hedraiophyllum* is retained in what was known until now as section *Moquiniastrum*.

The remaining three sections sensu Cabrera, sect. *Gochnatia*, sect. *Hedraiophyllum*, and sect. *Leucomeris*, are redefined resulting in the establishment of five sections: sect. *Anastraphioides*, sect. *Glomerata*, sect. *Gochnatia*, sect. *Leucomeris*, and sect. *Rotundifolia*.

Cabrera (1971) established two groups in his key to section *Gochnatia*, the "South American species" and the "Caribbean species." Species of this section have some characters in common, such as solitary or 2 to 3 capitula and caudate anther appendages, but other characters suggest that it should be separated into two sections: sect. *Anastraphioides* and sect. *Gochnatia*. The Caribbean species form the new section *Anastraphioides* clearly differentiated by spiny leaf margins (Fig. 1E), corollas very deeply 5-lobed (Fig. 4B), and pappus type A (Fig. 8A). The South American species, on the other hand, have predominantly ovate leaves with entire margins (Fig. 1A, F), corollas deeply 5-lobed, and pappus type B (Fig. 8B), and correspond to section *Gochnatia*.

The species *Gochnatia rotundifolia*, included by Cabrera in section *Gochnatia*, has characters that show a departure from the other sections of the genus such as glabrous and 3-veined leaves, white corollas, and anther appendages attenuate. It would approach Cabrera's section *Leucomeris* by its phyllaries glabrous with ciliate margins and conspicuous parallel veins, but *G. rotundifolia* lacks the involucre extending into the peduncle typical of this section. Consequently, this species is placed in the new, monotypic section *Rotundifolia*.

Gochnatia sect. *Hedraiophyllum* sensu Cabrera, which was already recognized by Cabrera (1971) to be artificial, is split off. Three species of this section, *G. arborescens*, *G. magna*, and *G. purpusii*, are placed in the new section *Glomerata* characterized by the exclusive presence of numerous capitula arranged in glomerulose pseudocorymbs (Fig. 2C). As mentioned above, the type species of section *Hedraiophyllum*, *G. cordata*, was moved to Cabrera's *Gochnatia* sect. *Moquiniastrum*. The remaining species of section *Hedraiophyllum*, *G. hypoleuca*, *G. palosanto*, and *G. smithii*, were placed in section *Leucomeris* largely based on their involucre with glabrous, conspicuously veined phyllaries, ciliolate at the margins, extending into the peduncle (Fig. 3I).

In summary, we propose the following eight sections for the genus *Gochnatia*: sect. *Anastraphioides*, sect. *Discoseris*, sect. *Glomerata*, sect. *Gochnatia*, sect. *Hedraiophyllum*, sect. *Leucomeris*, sect. *Pentaphorus*, and sect. *Rotundifolia*. This new infrageneric classification, with descriptions and a key to the sections, is shown in Appendix 2.

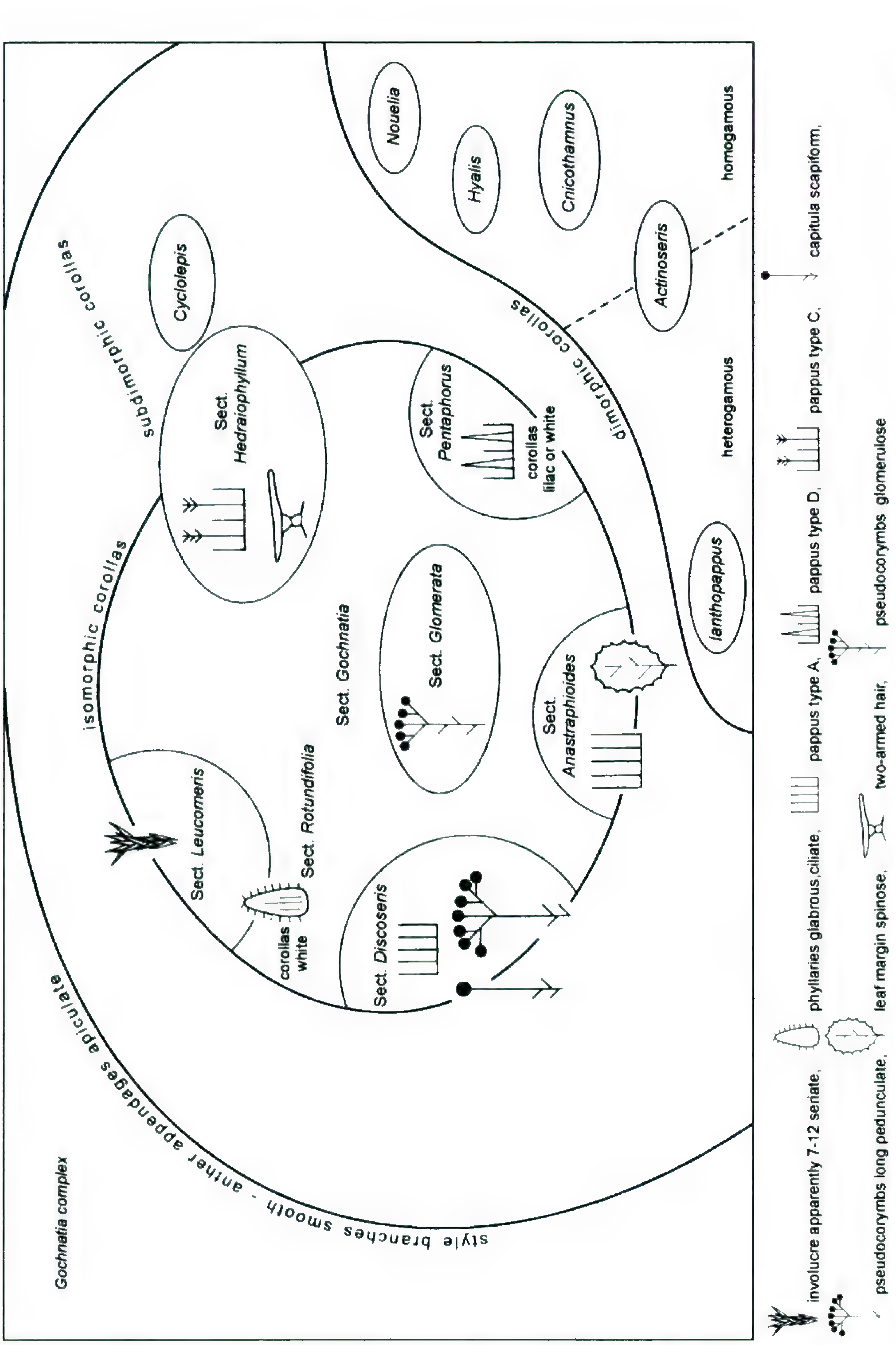

Figure 9. Main morphological characters defining the *Gochnatia* complex, allowing the distinction of *Gochnatia* from its related taxa, and also sections within *Gochnatia*.

THE *GOCHNATIA* COMPLEX

The combination of apiculate anther appendages and smooth style branches is exclusive to *Actinoseris, Cnicothamnus, Cyclolepis, Gochnatia, Hyalis, Ianthopappus,* and *Nouelia* within Mutisieae. Consequently, these genera are recognized here as the *Gochnatia* complex (Fig. 9). *Chucoa, Pleiotaxis,* and *Wunderlichia,* as already mentioned, differ in their styles and anthers.

Within the *Gochnatia* complex, the genus most morphologically similar to *Gochnatia* is *Cyclolepis.* This genus shares trichomes 2-armed, subdimorphic corollas, and gynodioecy with section *Hedraiophyllum,* which constitutes a pivotal group among the remaining species of *Gochnatia* and *Cyclolepis,* providing a "link" between both genera. *Cyclolepis,* however, can be distinguished from *Gochnatia* by its leafless, spiny branches, tubular, filiform female florets (Fig. $4G_1$), and pappus type E (Fig. 8E).

The hypothesis that a shrubby habit, large, homogamous, and solitary or few capitula, with yellow, and actinomorphic corollas represent primitive conditions in Asteraceae has been widely discussed and recognized (Maguire & Wurdack, 1957; Carlquist, 1976; Bremer, 1987, 1994; Pruski, 1991; Stuessy et al., 1996). From this point of view, most species of *Gochnatia* have a set of plesiomorphic characters when compared with the remaining genera of the complex. This hypothesis is consistent with Cabrera's (1977) idea that *Gochnatia* is the basal genus in a complex from which the other genera in the subtribe are derived.

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APPENDIX 1.

Index to specimens examined, with vouchers. Note: During preparation of this work, the new species *Gochnatia lanceolata* Beltrán & Ferreyra was published (Beltrán & Ferreyra, 2001). Specimens examined of this species (*Carolina 01*, isotype, US; *Torrico & Peca 336*, US) have pubescent styles and acute anther appendages, so this species must be excluded from *Gochnatia* and does not belong to the *Gochnatia* complex.

Actinoseris

A. angustifolia: BRAZIL. **Minas Gerais:** Jaboticatuba, *Hatschbach 28756* (LP); Serra do Cipó, *Hatschbach 29986* (LP).

A. polymorpha: BRAZIL. **Minas Gerais:** Serra de Cipó, *Brade 2007* (LP).

A. polyphylla: BRAZIL. **Minas Gerais:** Santa Ana do Riacho, *Hatschbach 35304* (LP).

A. radiata: BRAZIL. **Paraná:** Campo Largo, *Hatschbach 690* (LP).

A. stenophylla: BRAZIL. **Minas Gerais:** Santa Ana do Riacho, *Hatschbach 35388 & Koczicki* (LP).

Cyclolepis

C. genistoides: PARAGUAY. Chaco Paraguayo, *Rojas 7104* (LP). ARGENTINA. **Salta:** Quebrada de las Conchas, *Cabrera 3782* (LP). **Río Negro:** Gral. Conessa, *Correa 3172 & Nicora* (LP). **Salta:** La Candelaria, *Schreiter 6630* (LP). **San Juan:** La Laja, *Tinto 2038* (LP). **Neuquén:** Plotier, Banda, *Zardini & Kiesling 114* (LP).

Chucoa

C. ilicifolia: PERU. **La Libertad:** Santiago de Chuco, *López Miranda 1090* (LP).

Cnicothamnus

C. azafran: ARGENTINA. **Salta:** Serranías del Crestón, *Bortagaray 226* (LP). **Jujuy:** Santa Bárbara, *Cabrera et al. 26287* (LP).

C. lorentzii: ARGENTINA. **Salta:** Caldera, *Cabrera et al. 22576* (LP); Capital, Cerro San Bernardo, *Padaci 84* (LP); Abra de Santa Laura, *Ruiz Leal 14162* (LP); Capital, *Bonavía 61* (LP); camino de cornisa Salta-Jujuy, *Zardini 1292* (LP).

Gochnatia

G. amplexifolia: BRAZIL. **Minas Gerais:** Santa Ana do Riacho, *Hatschbach 35312* (LP).

G. arborescens: MEXICO. **Baja California:** Isla Cerralvo, *Johnston 4023* (LP); entre Santonio y Puerto de Bahía de los Muertos, *Wiggins 5632* (US); along the Pacific Coast, 14 mi. S of Pescadero, *Spjut & Edson 6085* (US).

G. arequipensis: PERU. **Arequipa:** Monte Chiwata, *Eyerdam & Beetle 22120* (LP).

G. argentina: ARGENTINA. **Tucumán:** Trancas, *Meyer 22421* (LP). **Entre Ríos:** Paracao, Paraná, *Schulz 173* (LP); Leales, *Venturi 703* (LP).

G. argyrea: BRAZIL. **Paraná:** Vila Velha, *Dusén 4035* (LP), *Dusén 9115* (G), *Hatschbach 9578* (LP).

G. attenuata: CUBA. **Oriente:** Sierra de Nipe, *Ekman 19174* (LP).

G. barrosii: BRAZIL. **Paraná:** Cianorte, *Hatschbach 16945* (LP). **Minas Gerais:** Ituitaba, *Macedo 1138* (LP). PARAGUAY. **Amambay:** Parque Nacional Cerro Corá, *Sancho 8* (LP).
G. blanchetiana: BRAZIL. **Ceará:** Serra do Araripe, *Gardner 1735* (K). **Goiás:** *Glaziou 21663* (G).
G. boliviana: BOLIVIA. **Santa Cruz:** Florida, *Cabrera & Gutiérrez 33804* (LP).
G. buchii: DOMINICAN REPUBLIC. Falda del Morro, Monte Cristo, *Jiménez 1598* (LP).
G. calcicola: CUBA. **Oriente:** Guantánamo, *Ekman 15764* (S).
G. cardenasii: ARGENTINA. **Jujuy:** Tafna, *Cordo & Ferrer 88-B-17* (SI).
G. cordata: ARGENTINA. **Entre Ríos:** Federación, *Burkart 23169 & Crespo* (LP); Santa Ana, *Serrano 6* (LP). BRAZIL. **Rio Grande do Sul:** Porto Alegre, *Rambo 545* (LP).
G. cowellii: CUBA. **Santa Clara:** Santa Clara, *Britton & Cowell 10183* (NY).
G. crassifolia: CUBA. **Oriente:** Baracoa, *Ekman 4023* (S).
G. cubensis: CUBA. **Oriente:** Sierra de Nipe, *Ekman 4767* (S), *9632* (S).
G. curviflora: BOLIVIA. **Tarija:** Tarija, *Fiebrig 2838* (LP). ARGENTINA. **Jujuy:** Humahuaca, *Meyer 21409* (LP). **Salta:** La Candelaria, *Schreiter 9409* (LP); La Candelaria, *Jeréz et al. 49120* (LP).
G. decora: MYANMAR. **Bhamo:** Lweji, *Maung Mya 5309* (LP).
G. densicephala: BRAZIL. **Rio de Janeiro:** Río de Janeiro, *Glaziou 11072* (K). **Minas Gerais:** Poços de Caldas, *Leoncini 88* (LP); Pico da Bandeira, *Shepherd 5771 et al.* (UEC).
G. discoidea: BRAZIL. **Bahia:** Igregia Velha, *Blanchet 3345* (LP).
G. discolor: BRAZIL. **Minas Gerais:** *Claussen 1301* (NY), *Claussen* in 1840 (K).
G. ekmanii: CUBA. Sin. loc., *Wright 2875* (GH).
G. enneantha: DOMINICAN REPUBLIC. Cordillera Central, Samaná, Los Haitises, *Ekman H-15498* (S).
G. floribunda: BRAZIL. **Minas Gerais:** Morro do Frío, *Gardner 4806* (K); Diamantina, *Hatschbach 30192* (US). **Distrito Federal:** Brasilia, *Hatschbach 43151* (NY).
G. foliolosa: CHILE. **Santiago:** Cerro Renca, *Cabrera 3451* (LP). **Valparaíso:** El Quisco, *Mahu 10336* (LP).
G. gardneri: BRAZIL. **Goyaz:** Capella da Passe, *Gardner 4183* (K).
G. glutinosa: ARGENTINA. **Tucumán:** Tafí, *Fabris 1343* (LP). **Mendoza:** Cerro de La Gloria, *King 183* (LP).
G. gomezii: CUBA. **Oriente:** Región de Moa, Cerro Miraflores, *Marie-Victorin et al. 21591* (GH).
G. hatschbachii: BRAZIL. **Minas Gerais:** Jaboticatubas, *Hatschbach 29951* (LP); Datas, *Hatschbach 30155* (LP).
G. haumaniana: BRAZIL. **Mato Grosso do Sul:** Ponta Porá, *Meyer 18770* (LP). PARAGUAY. **Amambay:** Sierra de Amambay, *Rojas 6575* (LP), Rojas [herb. *Hassler 9752*] (G); Est. Los cinco hermanos, *Sancho 41* (LP).
G. hypoleuca: MEXICO. **Hidalgo:** Cañada del Vaquero, *González Quintero 3215* (LP). **Coahuila:** Sierra Gavia, *Johnston 7223* (LP).
G. ilicifolia: BAHAMAS ISLANDS. **Andros Island:** Coppice, *Small & Carter 8526* (K).
G. intertexta: CUBA. **Pinar del Río:** Cajalbana, *Alain A-1680* (NY).
G. magna: MEXICO. **San Luis Potosí:** *Cronquist 11277* (NY); Queretaro, 5 km SW Jalpan, *Fernández 3666* (NY).
G. mantuensis: CUBA. **Pinar del Río:** Guane, *Shafer 11208* (LP).
G. microcephala: CUBA. **Oriente:** Boca Guantánamo a Mantua, *Bro. Hioram 4874* (NY).
G. mollissima: BRAZIL. **Rio Grande do Sul:** *Malme 648* (S); pr. Santa María, *Malme 1261* (S).
G. montana: CUBA. **Pinar del Río:** Guane, *Ekman 18725* (S).
G. obtusifolia: CUBA. **Oriente:** Southern Baracoa region, Mesa de Prada, *León 11963* (NY).
G. oligantha: REPUBLICA DOMINICANA. Monte Cristi, N of Villa Isabel, *Jiménez 3614* (US).
G. oligocephala: BRAZIL. **Bahia:** Serra do Jacobina, *Blanchet 3288* (US); Río Branco, *Curran 284* (NY), *Salzmann s.n.* (G).
G. orbiculata: BRAZIL. **São Paulo:** Moóca, *Brade 5523* (US). **Rio Grande do Sul:** Guaiba, *Sancho 48* (LP); río Jaquety hills, *Tweedie 998* (K).
G. palosanto: ARGENTINA. **Jujuy:** San Pedro, *Cabrera & Fabris 21157* (LP). **Tucumán:** Vipos, Trancas, *Venturi 1296* (LP), *Schreiter* in 1925 (LP).
G. paniculata: BRAZIL. **Minas Gerais:** Massa, *Brade 13550* (LP), *Gardner 4810* (US).
G. parvifolia: CUBA. **Oriente:** Barren Savannas, *Shafer 2938* (NY).
G. patazina: PERU. **La Libertad:** Pataz entre Huaylillas y Tayabamba, *López & Sagástegui 3409* (LP).
G. pauciflosculosa: BAHAMAS ISLANDS. **Fortune Island:** *Eggers 3866* (K); Mariguana Island, 10 mi. W of Abraham Bay, *Wilson 7428* (K).
G. picardae: HAITI. Massif de la Selle, croix-des Bauquets, gorge of Grande-Rivière de cul-de sac, *Ekman H-5385* (K).
G. polymorpha: BRAZIL. **Rio de Janeiro:** Tijuca, *Glaziou* in 1876 (LP). **São Paulo:** Paranaiba do Sul, *Hashimoto 624* (LP). **Rio Grande do Sul:** *Pereira 8609 & Pabst 7984* (LP). PARAGUAY. **Amambay:** *Sancho 26*, *Sancho 32* (LP). **San Pedro:** Lima, *Pedersen 8587* (LP).
G. pulchra: BRAZIL. **São Paulo:** Campos de Emas, *Cabrera 12311* (LP); Ityrapina, *Gehrt 8296* (LP).
G. purpusii: MEXICO. **Puebla:** Tehuacán, *Purpus 4248* (NY).
G. ramboi: BRAZIL. **Santa Catarina:** Xanxeré, *Rambo 50005* (S). **Rio Grande do Sul:** Palmeira, *Rambo 51961* (LP).
G. recurva: CUBA. **Oriente:** entre Moa y Punta Andén, *León 20946* (LP).
G. rotundifolia: BRAZIL. **São Paulo:** Capital, Jabaquara, *Handro 157* (LP); Vila Esperança, *Joly 596* (LP).
G. rusbyana: BOLIVIA. **Yungas:** *Bang 2252* (LP). PERU. **Cusco:** Alto Urumbamba, *Zamalloa 2015* (LP).
G. sagraeana: CUBA. **Habana:** *León 7094* (NY); Vedado, *Alain 2532* (NY).
G. shaferi: CUBA. **Oriente:** La Caridad, *López Figueiras 1738* (NY).
G. smithii: MEXICO. **Oaxaca:** Cuesta de Coyula, *Conzatti 4135* (US).
G. sordida: BRAZIL. **Paraná:** Ponta Grossa, *Hatschbach 17422* (LP); Senges, *Hatschbach 27167* (K).
G. spectabilis: INDIA. **Uttar Pradesh:** Rajpur, Dehra Dun District, *Galrola 32* (LP).

G. tortuensis: HAITI. Presquile du Nord-Ouest, Port-de Paix, *Ekman H-3553* (S).

G. vargasii: PERU. **Apurimac:** Abancay, *Vargas 16317* (LP).

G. velutina: BRAZIL. **Paraná:** Ponta Grossa, Vila Velha, *Hatschbach 23447* (LP), *López 4364* (LP), *Smith & Klein 14885* (LP).

G. vernonioides: PERU. **Amazonas:** Chachapoyas, Tingo, *Ferreyra 7097* (LP); entre Chachapoyas y Leimebamba, *López et al. 4364* (LP). **La Libertad:** Bolívar, *Infantes 1701* (LP), *López & Sagástegui 3354* (LP).

Hyalis

H. argentea: ARGENTINA. **Mendoza:** Tupungato, *Ruiz Leal 3701* (LP).

H. lancifolia: ARGENTINA. **Chaco:** San Fernando, *Cabrera 4083* (LP), *Schinini 16098* (LP).

Ianthopappus

I. corymbosus: ARGENTINA. **Corrientes:** Paso Troncón, *Palacios & Cuezzo 2304* (LP).

Nouelia

N. insignis: CHINA. *Maire 2516* (NY). **Yunnan:** *l' Abbe Delavay 2498* (US), *Rock 11714* (US).

Pleiotaxis

P. dewevrei: DEMOCRATIC REPUBLIC OF CONGO. Lukulu, *de Hitte 288* (US).

P. eximia: DEMOCRATIC REPUBLIC OF CONGO. Tshinloingwe (Hout Katanga), *Rolyns 1836* (US). ZIMBABWE. 20 km de Mangula, *Lavranos 22745* (US).

P. huillensis: ANGOLA. Huila, Hampata, *Gossweiler 10780* (US).

P. pulcherrima: ANGOLA. Distr. do Cuanza Sul, Seles, *Gossweiler 9367* (US).

P. rogersii: ZAIRE—DEMOCRATIC REPUBLIC OF CONGO. Elisabethville, *Rolyns 1568* (US).

Wunderlichia

W. azulensis: BRAZIL. **Minas Gerais:** Pedra Azul, *Harley et al. 25209* (MO).

W. crulsiana: BRAZIL. **Goiás:** Chapada dos Veadeiros, *Ratter et al. 2615* (MO).

W. mirabilis: BRAZIL. **Goiás:** Serra do Cristais, *Irwin et al. 9913* (NY); about 52 km W of Alto Paraiso, *Martinelli & Stutts 999* (NY).

APPENDIX 2.

New infrageneric classification of *Gochnatia*.

KEY TO THE SECTIONS OF *GOCHNATIA*

1. Pappus type A (all bristles are thin and have the same length and width) and/or pappus type B (all bristles are thin and have the same width, but about half are shorter) 2
1′. Pappus type C (all bristles are thin and have the same width, half of them are shorter, and the longer are plumose at the apex) or pappus type D (half of the bristles are long and wide, and the other half are short and thin) 7
2(1). Subshrubs; capitula solitary, very long-pedunculate, or arranged in scapiform pseudocorymbs .... *G.* sect. *Discoseris*
2′. Trees or shrubs; capitula short-pedunculate or sessile 3
3(2). Involucral phyllaries dorsally glabrous or subglabrous and ciliolate at the margins 4
3′. Involucral phyllaries dorsally tomentose and not ciliolate at the margins 5
4(3). Capitula arranged in glomerulose pseudocorymbs, pseudoracemes, or pseudopanicles; phyllaries extending into the peduncle .... *G.* sect. *Leucomeris*
4′. Solitary capitula; phyllaries not extending into the peduncle .... *G.* sect. *Rotundifolia*
5(3). Solitary capitula or 2 or 3 6
5′. Capitula in glomerulose pseudocorymbs .... *G.* sect. *Glomerata*
6(5). Leaves spiny; corollas deeply to very deeply lobed .... *G.* sect. *Anastraphioides*
6′. Leaves not spiny; corollas deeply lobed .... *G.* sect. *Gochnatia*
7(1). Pappus type C; plants not glandulose, with 2-, and 3- to 5-armed hairs; gynodioecious or polygamous dioecious; corollas subdimorphic (isomorphic), 9–15(50) .... *G.* sect. *Hedraiophyllum*
7′. Pappus type D; plants glandulose; monoecious; corollas isomorophic, 5 (3, 7, or 10–20) .... *G.* sect. *Pentaphorus*

Gochnatia sect. **Anastraphioides** Jervis ex S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia ilicifolia* Less.

Arbores vel frutices, foliis alternis, spinoso-dentatis vel integerrimis. Capitula apicibus ramulorum, solitaria vel 2–3, sessilia. Involucrum campanulatum vel turbinatum. Flores 4–150, lutei vel aurantiaci, isomorphi, hermaphroditi, corolla tubulosa pentasecta vel profunde pentasecta. Antherae appendicibus connectivalibus caudatis vel abruptis, appendicibus basalibus integerrimis vel laciniatis. Pappus uniseriatus vel biseriatus.

Shrubs or small *trees*, monoecious. *Leaves* alternate, petiolate or shortly petiolate; obovate, oblong, or elliptic with margins spinose-dentate (rarely entire); pinnately veined; upper surface generally glabrous, lower surface densely tomentose (with flagellate hairs). *Capitula* homogamous, discoid, sessile, solitary at the tip of the branches (rarely 2 or 3). Involucre campanulate or turbinate. *Phyllaries* in 4 to 10(15) series, dorsally tomentose. *Florets* 4 to 150, yellow or orange, hermaphroditic, isomorphic, tubulose, deeply to very deeply 5-lobed. Anthers with appendages caudate (rarely abruptly apiculate), and commonly smooth, occasionally laciniate tails. Style bilobate or shortly bifid; style branches rounded, dorsally glabrous. *Cypselas* with duplex hairs and commonly capitate glandular hairs (rarely with flagellate hairs). *Pappus* uniseriate with all bristles of the same length (rarely biseriate with a reduced number of outer short bristles) all thin.

Twenty-six species: *G. attenuata*, *G. buchii*, *G. calcicola*, *G. cowellii*, *G. crassifolia*, *G. cubensis*, *G. ekmanii*, *G. elliptica*, *G. enneantha*, *G. gomezii*, *G. ilicifolia* (type species), *G. intertexta*, *G. maisiana*, *G. mantuensis*, *G. microcephala*, *G. montana*, *G. obtusifolia*, *G. oligantha*, *G. parvifolia*, *G. pauciflosculosa*, *G. picardae*, *G. recurva*, *G. sagraeana*, *G. shaferi*, *G. tortuensis*, *G. wilsonii*.

Distribution. Bahamas Islands, Cuba, Haiti, Dominican Republic, Puerto Rico.

Observations. As pointed out by Jervis (1954) and Ca-

brera (1971), *Anastraphia* D. Don (Trans. Linn. Soc. London 16: 295. 1830) is considered an unknown genus because its type (*Anastraphia ilicifolia* D. Don based on a "Joannes Fraser" specimen in the Lambert herbarium) has never been located. The original diagnosis of *Anastraphia* does not agree with the later interpretation of the genus by de Candolle (1838: 26).

Gochnatia sect. **Discoseris** (Endlicher) Cabrera, Revista Mus. La Plata 12, Secc. Bot. 66: 150. 1971. *Seris* Less., non Willd. 1807, Linnaea 5: 253. 1830. *Seris* sect. *Discoseris* Endl., Gen. Pl.: 483. 1838. *Richterago* Kuntze, Rev. Gen. Pl. 1: 360. 1891. *Discoseris* (Endl.) T. Post & Kuntze, Lex. Gen. Phan.: 181. 1904, nom. superfl. TYPE: *Seris discoidea* Less. (= *Gochnatia discoidea* (Less.) Cabrera).

Subshrubs, monoecious. *Leaves* alternate, petiolate; ovate to ovate-elliptic with margins entire or denticulate; pinnately veined; glabrous or tomentose on both sides (with flagellate hairs). *Capitula* homogamous, discoid, long-pedunculate and solitary or arranged in scapose pseudocorymbs. Involucre campanulate to turbinate. *Phyllaries* in 4 or 5 series, dorsally tomentose. *Florets* numerous (ca. 30), yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate and laciniate tails. Style shortly bifid; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* uniseriate with all bristles of the same length and thin.

Three species: *G. amplexifolia*, *G. discoidea* (type species), *G. suffrutescens*.

Distribution. Southeastern Brazil.

Gochnatia sect. **Glomerata** S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia arborescens* T. S. Brandegee (selected here).

Arbores vel frutices, foliis alternis, integerrimis. Capitula pauca, sessilia vel subsessilia, apicibus ramulorum glomerata. Involucrum campanulatum. Flores 12–50, lutei, isomorphi, hemaphroditi, corollis tubulosis, pentasectis. Antherae appendicibus connectivalibus attenuatis vel abruptis, appendicibus basalibus integerrimis. Pappus biseriatus vel uniseriatus.

Small *trees* or shrubs, monoecious. *Leaves* alternate, shortly petiolate; ovate to elliptic with margins entire or denticulate; pinnately veined; upper surface glabrous or tomentulose, lower surface usually densely tomentose (with flagellate hairs). *Capitula* homogamous, discoid, sessile or subsessile, few together in terminal glomerulose pseudocorymbs. Involucre campanulate. *Phyllaries* in 5 or 6 series (rarely 8 to 10), dorsally tomentose or glabrous. *Florets* 12 to 20 (rarely ca. 50), yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate (rarely attenuate) and smooth tails. Style shortly bifid or bilobate; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer short bristles (rarely uniseriate with all bristles of the same length), all thin.

Three species: *G. arborescens* (type species), *G. magna*, *G. purpusii*.

Distribution. Northern Mexico.

Gochnatia Kunth sect. **Gochnatia,** Nov. Gen. Sp. 4: 15. 1818. TYPE: *Gochnatia vernonioides* Kunth.

Shrubs, monoecious. *Leaves* alternate, shortly petiolate; ovate or ovate-elliptic with margins entire (rarely denticulate); pinnately, occasionally subtri-veined; upper surface generally glabrous or tomentulose, lower surface densely tomentose (with flagellate hairs). *Capitula* homogamous, discoid, sessile or short-pedunculate, solitary (rarely 2 or 3). Involucre oblong to campanulate. *Phyllaries* in 3 to 7 series, dorsally tomentose or only tomentose above. *Florets* 7 to 40, yellow, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages caudate, more rarely abruptly apiculate, and laciniate tails. Style shortly bifid; style branches rounded, dorsally glabrous. *Cypselas* with duplex hairs and usually glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer, short bristles, all thin.

Seven species: *G. arequipensis*, *G. boliviana*, *G. cardenasii*, *G. curviflora*, *G. patazina*, *G. vargasii*, *G. vernonioides* (type species).

Distribution. Andes of Peru, Bolivia, and northwestern Argentina.

Gochnatia sect. **Hedraiophyllum** (Lessing) DC., Prodr. 7(1): 24. 1838. *Gochnatia* subg. *Hedraiophyllum* Less., Syn. Gen. Compos.: 103. 1832. TYPE: *Gochnatia cordata* Less.
Gochnatia sect. *Moquiniastrum* Cabrera, Revista Mus. La Plata 12, Secc. Bot. 66: 73. 1971. TYPE: *Spadonia polymorpha* Less. (= *G. polymorpha* (Less.) Cabrera).

Shrubs or *trees*, commonly gynodioecious or polygamous dioecious. *Leaves* alternate, petiolate or shortly petiolate; ovate, elliptic (rarely linear or cordate) with margins entire, rarely denticulate; pinnately veined; upper surface glabrous (rarely tomentose), lower surface densely tomentose (with 2-, 3- to 5-armed hairs, occasionally flagellate). *Capitula* heterogamous (homogamous), disciform (rarely discoid), subsessile to pedunculate, numerous arranged in terminal and usually loose leafy pseudopanicles. Involucre oblong to campanulate. *Phyllaries* in 3 or 4 series, dorsally tomentose. *Florets* 9 to 15(50), creamy or white, tubulose, deeply 5-lobed, subdimorphic (occasionally isomorphic); functionally female, corollas slightly zygomorphic, with straight lobes; hermaphroditic, actinomorphic, with resupinate lobes. Anthers with appendages abruptly apiculate and laciniate or smooth tails. Style shortly bifid (rarely bilobate); style branches rounded, dorsally glabrous. *Cypselas* with duplex, glandular, and flagellate hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer short bristles, all thin, and the longest are plumose at the apex.

Twenty-one species: *G. argentina*, *G. argyrea*, *G. barrosii*, *G. blanchetiana*, *G. cordata* (type species), *G. densicephala*, *G. discolor*, *G. floribunda*, *G. gardneri*, *G. hatschbachii*, *G. haumaniana*, *G. mollissima*, *G. oligocephala*, *G. orbiculata*, *G. paniculata*, *G. polymorpha*, *G. pulchra*, *G. ramboi*, *G. rusbyana*, *G. sordida*, *G. velutina*.

Distribution. Andes of Peru and Bolivia, eastern Brazil, Paraguay, Uruguay, and central-eastern Argentina.

Gochnatia sect. **Leucomeris** (D. Don) Cabrera, Revista Mus. La Plata 12, Secc. 66: 128. 1971. *Leucomeris* D. Don, Prodr. Fl. Nepal.: 169. 1825. *Gochnatia* subg. *Leucomeris* (D. Don) Less., Syn. Gen. Compos.: 103. 1832. TYPE: *Gochnatia spectabilis* (D. Don) Less. (= *Leucomeris spectabilis* D. Don).

Trees or *shrubs*, monoecious. *Leaves* alternate, shortly petiolate; elliptic, margins entire or denticulate; pinnately (3-)veined; upper surface generally glabrous to tomentose, lower surface densely tomentose (with flagellate hairs) or glabrous on both sides. *Capitula* homogamous, discoid, subsessile, many in glomerules, arranged in terminal leafy pseudoracemes, pseudopanicles, or pseudocorymbs. Involucre campanulate, oblong or turbinate. *Phyllaries* in 3 to 6(7) series, dorsally glabrous with ciliolate margins, extending to the peduncle. *Florets* 4 to 6 (8 to 12), white (rarely yellow), hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages attenuate (rarely abruptly apiculate) and laciniate tails (rarely smooth). Style bilobate or shortly bifid, style branches obtuse or rounded, dorsally glabrous. *Cypselas* with duplex hairs and commonly with glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer short bristles, all thin.

Five species: *G. hypoleuca, G. palosanto, G. smithii, G. decora, G. spectabilis* (type species).

Distribution. Mexico, Brazil, Andean region of Bolivia and Argentina, and southeastern Asia.

Gochnatia sect. **Pentaphorus** (D. Don) DC., Prodr. 7(1): 24. 1838. *Pentaphorus* D. Don, Trans. Linn. Soc. London 16: 296. 1830. *Gochnatia* subg. *Pentaphorus* (D. Don) Hook. & Arn., Comp. Bot. Mag. 1: 108. 1835. TYPE: *Gochnatia foliolosa* D. Don ex Hook. & Arn.

Shrubs, monoecious. *Leaves* alternate, sessile; linear-ovate or linear-obovate with margins entire or upper portion denticulate; pinnately or three-veined; upper and lower surfaces glandulate (with or without flagellate hairs). *Capitula* homogamous, discoid, sessile or subsessile, numerous in leafy glomerulose pseudoracemes. Involucre campanulate. *Phyllaries* in 4 to 6 series, dorsally glabrous or tomentulose with ciliolate margin. *Florets* 5 (rarely 3, 7, or 10 to 20), white or lilac, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages abruptly apiculate and smooth or laciniate tails. Style bilobate or shortly bifid; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* biseriate of numerous scabrid bristles, half of them relatively wide and long, and the others short and thin.

Two species: *G. foliolosa, G. glutinosa* (type species).

Distribution. Western Argentina and central Chile.

Gochnatia sect. **Rotundifolia** S. E. Freire, L. Katinas & G. Sancho, sect. nov. TYPE: *Gochnatia rotundifolia* Less. (selected here).

Frutices, foliis alternis, integerrimis vel denticulatis. Capitula apicibus ramulorum solitaria, sessilia. Involucrum campanulatum; bracteis involucralibus subglabris, margine ciliatis. Flores multi, albi, isomorphi, hermaphroditi, corollis tubulosis, pentasectis. Antherae appendicibus connectivalibus attenuatis apiculatis, appendicibus basalibus laciniatis. Pappus biseriatus, setosus.

Shrubs, monoecious. *Leaves* alternate, shortly petiolate; broadly elliptic with margins entire to denticulate; three-veined, glabrous on both surfaces at maturity (young leaves with flagellate hairs). *Capitula* homogamous, discoid, sessile, solitary. Involucre campanulate. *Phyllaries* in 4 or 5 series, dorsally subglabrous with ciliolate margin. *Florets* ca. 50, white, hermaphroditic, isomorphic, tubulose, deeply 5-lobed. Anthers with appendages attenuate and laciniate tails. Style bilobate; style branches rounded, dorsally glabrous. *Cypselas* with duplex and glandular hairs. *Pappus* biseriate of numerous scabrid bristles, with a reduced number of outer, short bristles, all thin.

One species: *G. rotundifolia.*

Distribution. Southeastern Brazil.

EL GÉNERO *QUERCUS* (FAGACEAE) EN EL ESTADO DE MÉXICO[1]

Silvia Romero Rangel[2], Ezequiel Carlos Rojas Zenteno[3] y María de Lourdes Aguilar Enríquez

Resumen

Con base en trabajo de campo y de herbario, se reconocen 23 especies de *Quercus* para el Estado de México. Diez pertenecen a la sección *Quercus* y 13 a la sección *Lobatae*. Quince de las especies son endémicas de México, siete están distribuidas hasta Centro América y sólo *Quercus rugosa* se encuentra en el norte de la frontera mexicana, en los Estados Unidos. El trabajo incluye una clave dicotómica y descripciones morfológicas de cada uno de los taxa. Adicionalmente, para cada especie se proporcionan datos etnobotánicos, fenológicos y ecológicos.

Abstract

Based on field and herbarium work, in this paper 23 species of *Quercus* are recognized for the State of México. Ten of the species belong to section *Quercus* and 13 to section *Lobatae*. Fifteen of the species are endemic to Mexico, seven extend to Central America, and only *Quercus rugosa* is found north of the Mexican border in the United States. The paper includes a dichotomous key and morphological descriptions for all the taxa, as well as ethnobotanical, phenological, and ecological data.

Key words: Fagaceae, Mexico, *Quercus*.

El género *Quercus* se distribuye mundialmente en zonas templadas y subtropicales del hemisferio norte. Se calcula que está conformado aproximadamente por 500 especies distribuidas mundialmente. México es el país que posee el mayor número de especies del mundo, entre 135 y 150 (Nixon, 1993b), distribuidas en las zonas montañosas de todos los estados y territorios, a excepción del sur en Yucatán y Quintana Roo (Rzedowski, 1978).

A las especies del género *Quercus* se les encuentra formando bosques de encino, comunidades muy características de las zonas montañosas de México. De hecho junto con los miembros del género *Pinus* constituyen la mayor parte de la cubierta vegetal de áreas de clima templado y semihúmedo; sin embargo no se limitan a estas condiciones, pues penetran en regiones de clima caliente formando también bosques, no faltan en las francamente húmedas, siendo elementos del bosque tropical perennifolio y bosque mesófilo de montaña, y aún existen en las semiáridas siendo parte del matorral xerófilo, asumiendo con frecuencia forma arbustiva (Rzedowski, 1978).

Existen dos trabajos que intentan registrar las especies de la entidad en estudio. Uno es de Martínez (1954) titulado "Encinos del Estado de México"; en él se refieren 45 especies, número que se ha modificado por la gran cantidad de sinónimos. El otro es de Espinosa (Rzedowski & Rzedowski, 1979), quien publicó, dentro de la "Flora fanerogámica del Valle de México", los encinos de esta zona. Una porción de esta región pertenece al Estado de México; en él se mencionan 13 especies para el área de estudio. Otros trabajos importantes que consideran especies de la entidad estudiada son los de Muller y McVaugh (1972), McVaugh (1974) y de Aguilar y Romero (1995).

El Estado de México ocupa una superficie de 22,500 km^2 y está comprendido en dos provincias fisiográficas: la del Eje Neovolcánico que abarca la mayor parte de la superficie del norte, con altitudes

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Esta comunicación pertenece al proyecto encinos de México que se lleva a cabo en la UBIPRO de la UNAM Campus Iztacala.

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que van de 2000 a 5452 m y la de la Sierra Madre del Sur que abarca el extremo SE, donde las altitudes son de 600 a 3000 m (INEGI, 1987).

Los encinos son abundantes en las regiones montañosas de la entidad estudiada, formando parte de los bosques de coníferas, bosques de *Quercus*, bosques mixtos de *Pinus–Quercus* y *Cupressus–Quercus*; aunque también habitan en otras comunidades tales como bosque mesófilo de montaña, bosque tropical caducifolio, no faltando en matorral xerófilo, bosque de galería y pastizal.

Quercus es considerado como un género taxonómicamente complicado, debido a su gran variabilidad morfológica, a la capacidad de formar híbridos y a que sus estructuras reproductivas no se han estudiado lo suficiente (Romero et al., 2000). Esto ha llevado a la existencia de una gran cantidad de sinónimos.

Materiales y Métodos

El trabajo se basó fundamentalmente en la revisión y estudio de los ejemplares existentes en los herbarios CHAPA, CODAGEM, ENCB, INIF, IZTA y MEXU.

Se obtuvo la variación morfológica regional de los ejemplares citados y de las observaciones realizadas en campo por los autores.

Para determinar la aplicación de los nombres se revisaron las descripciones originales y los ejemplares tipo provenientes de herbarios; cuando estos últimos no estuvieron disponibles para su análisis, se utilizaron en su lugar las fotografías de los tipos contenidas en Trelease (1924). Estos últimos y los herbarios donde están depositados se citan como lo hace dicho autor. En este trabajo se incluyen sólo los sinónimos encontrados para el Estado de México.

Las descripciones morfológicas se realizaron de acuerdo al formato del tratamiento del género *Quercus* para la *Flora Novo-Galiciana* (McVaugh, 1974).

El hábitat, las descripciones morfológicas, la distribución geográfica y los dibujos de las especies están basados en los ejemplares revisados para cada especie.

Tratamiento Taxonómico para el Género *Quercus* en el Estado de México

Son 23 las especies reconocidas en este trabajo; 10 pertenecen a la sección *Quercus* y 13 a la sección *Lobatae*, de acuerdo a la clasificación del género *Quercus* propuesta por Nixon (1993a).

Quercus L., Syst. Pl. ed. 2, II, 994. 1753. TYPE: *Quercus robur* L. (fide ING). [Sinonimia completa en Camus (1938).]

Árboles o arbustos; monoicos; yemas foliares reunidas en las puntas de las ramas; estípulas subuladas o liguladas, generalmente decíduas, a veces persistentes, más bien asociadas con las yemas que con las hojas; hojas alternas, generalmente pecioladas, nunca totalmente sésiles; amentos masculinos largos y colgantes, flores con el cáliz 5-lobulado, fusionado a un perianto que envuelve a los estambres; estambres de 5 a 10, libres, con anteras cortas y filamentos delgados; flores femeninas en forma de racimo reducido con un raquis leñoso corto o largo y con una o varias flores, el cáliz con 6 lóbulos que se adhieren a la base de los estilos y se fusionan en un tubo; pistilo de 3 carpelos que forman un ovario trilocular, cada lóculo con 2 óvulos; estilos 3, libres; fruto unilocular con una semilla, los otros 5 óvulos son abortados; semilla envuelta en una cubierta rígida formando la bellota que está protegida parcialmente en su base por una cúpula cubierta de escamas; N = 12.

I. Quercus sect. **Quercus**

Base del perianto femenino adnado al ovario; estilos cortos y anchos; pared interna del endocarpo glabra; escamas de la cúpula aquilladas, engrosadas en la base; dientes de las hojas mucronados; óvulos abortivos basales.

1. *Q. deserticola* Trel.
2. *Q. frutex* Trel.
3. *Q. glabrescens* Benth.
4. *Q. glaucoides* M. Mart. & Gal.
5. *Q. laeta* Liebm.
6. *Q. magnoliifolia* Née
7. *Q. obtusata* Humb. & Bonpl.
8. *Q. peduncularis* Née
9. *Q. rugosa* Née
10. *Q. splendens* Née

II. Quercus sect. **Lobatae** Loudon., Hort. Brit. 385. 1830. TYPE: *Quercus aquatica* Walt. (lectotipo, designado por Nixon (1993a)).

Base del perianto femenino libre; estilos por lo general alargados, lineares; pared interna del pericarpo pubescente; escamas de la cúpula, no aquilladas, no engrosadas en la base; dientes de las hojas, por lo general aristados; óvulos abortivos en posición apical o lateral.

11. *Q. acutifolia* Née
12. *Q. candicans* Née
13. *Q. castanea* Née

14. *Q. conspersa* Benth.
15. *Q. crassifolia* Humb. & Bonpl.
16. *Q. crassipes* Humb. & Bonpl.
17. *Q. dysophylla* Benth.
18. *Q. elliptica* Née
19. *Q. hintonii* E. F. Warb.
20. *Q. laurina* Humb. & Bonpl.
21. *Q. mexicana* Humb. & Bonpl.
22. *Q. scytophylla* Liebm.
23. *Q. urbanii* Trel.

De los 45 nombres citados en la bibliografía para el Estado de México, 20 resultaron ser sinónimos de las especies tratadas en este trabajo y las cinco siguientes las hemos considerado no existentes en la entidad estudiada; se indican las secciones a las que pertenecen (Nixon, 1993a).

I. *QUERCUS* SECT. *QUERCUS*

Quercus sanchez-colinii Mart. Citada por Martínez (1954), seguramente corresponde a una variación de *Q. laeta* debido a la similitud morfológica entre ellas. Sin embargo no se han vuelto a colectar ejemplares con hojas de borde ondulado como las observadas en el tipo de la primera especie.

Quercus repanda Humb. & Bonpl. Citada por Espinosa (Rzedowski & Rzedowski, 1979), fue confundida con *Q. frutex* debido a que ambas presentan formas arbustivas y similitud en la morfología de la hoja. Una diferencia que hace posible separarlas es que *Q. frutex* posee pubescencia en el envés de las hojas que permite ver la epidermis, formada por tricomas estrellado-estipitados con menos de nueve rayos; mientras que *Q. repanda* posee pubescencia muy densa que no deja ver la epidermis, formada por tricomas estrellados sésiles o cortamente estipitados con más de 15 rayos.

II. *QUERCUS* SECT. *LOBATAE*

Quercus affinis Schiede. Citada por Martínez (1954), es muy similar a *Quercus laurina*, con la que fue confundida. La primera se distingue por poseer yemas foliares de forma conoidal, base de las hojas cuneada, nervaduras planas, y distribución en altitudes menores a los 2400 m; mientras que *Q. laurina* posee las yemas ovoides, la base de la hoja atenuada o redondeada, nervaduras realzadas y distribución en altitudes mayores a los 2200 m.

Quercus salicifolia Née fue confundida también por Martínez (1954) con *Q. laurina*. La primera presenta de 15 a 25 nervaduras primarias en las hojas y se distribuye en la vertiente del Pacífico, en altitudes de 600–2000 m. La segunda posee un número menor de nervaduras primarias (4 a 12); se le encuentra en estados de la vertiente del Pacífico y del centro del país, en altitudes de 2240–3150 m.

Quercus aristata Hook & Arn. Citada por Martínez (1954), no se encontró en los herbarios revisados, ni se logró colectar en los sitios referidos en la descripción original.

CLAVE DE LAS ESPECIES DE *QUERCUS* DEL ESTADO DE MÉXICO, MÉXICO

1a. Hojas de borde entero, algunas veces mucronadas o aristadas en el ápice, pero sin dientes laterales.
- 2a. Envés de las hojas glabro o con tricomas concentrados en las axilas de las nervaduras o a lo largo de las mismas, frecuentemente glandular.
  - 3a. Hojas comunmente glaucas, ápice nunca aristado; cúpula con escamas engrosadas en la base; pared interna del pericarpo glabra.
    - 4a. Superficies maduras glabras por completo o con algunos tricomas cerca de la base, nervaduras rojizo amarillentas .... 4. *Q. glaucoides*
    - 4b. Superficies maduras con tricomas a lo largo de la nervadura central, nervaduras verdes .... 10. *Q. splendens*
  - 3b. Hojas no glaucas, ápice comunmente aristado; escamas de la cúpula no engrosadas en la base; pared interna del pericarpo lanosa.
    - 5a. Ramillas y pecíolos densamente pubescentes .... 18. *Q. elliptica*
    - 5b. Ramillas y pecíolos glabrescentes o glabros.
      - 6a. Hojas de 11–17 cm de largo; con el envés con abundantes tricomas glandulares .... 14. *Q. conspersa*
      - 6b. Hojas de 5–11 cm de largo; con escasos tricomas glandulares .... 20. *Q. laurina*
- 2b. Envés de la hoja pubescente, con los tricomas uniformemente distribuidos, sobre la lámina, no concentrados en las axilas de las nervaduras o a lo largo de las mismas.
  - 7a. Ápice de la hoja aristado; pared interna del pericarpo lanoso.
    - 8a. Envés de la hoja con tricomas contortos, epidermis papilosa .... 21. *Q. mexicana*
    - 8b. Envés de la hoja con tricomas no contortos; epidermis ampulosa.
      - 9a. Pubescencia amarilla .... 17. *Q. dysophylla*
      - 9b. Pubescencia grisácea.
        - 10a. Nervaduras conspicuamente elevadas en el envés, de 5–12 en cada lado, bellota de 5–15 mm de largo .... 13. *Q. castanea*
        - 10b. Nervaduras ligeramente elevadas en el envés, de 10–19 en cada lado, bellota de 12–30 mm de largo .... 16. *Q. crassipes*

7b. Ápice de la hoja con un mucrón; pared interna del pericarpo glabra.
11a. Arbustos rizomatosos de 0.40–2.5 m de alto; hojas comunmente de 2–4.5 cm de largo; cúpula del fruto de 7–13 mm diám .... 2. *Q. frutex*
11b. Árboles pequeños de 2–7 m de alto; hojas comunmente de 4–7.5 cm de largo; cúpula del fruto de 14–17 mm diám .... 1. *Q. deserticola*
1b. Hojas con el borde dentado, ondulado o con los bordes aristados o mucronados.
12a. Hojas con el borde ondulado o con dientes mucronados, nunca aristado.
13a. Envés de la hoja glabro, glabrescente o con tricomas concentrados en las axilas de las nervaduras o a lo largo de las mismas.
14a. Hojas con el envés glauco.
15a. Superficies maduras glabras por completo; árboles de 4–10 m de alto; estípulas de 4–5 mm de largo .... 4. *Q. glaucoides*
15b. Superficies maduras con tricomas que tienden a concentrarse en la nervadura central; árboles de 10–15 m de alto; estípulas de 5–8 mm de largo .... 10. *Q. splendens*
14b. Hojas con el envés no glauco .... 3. *Q. glabrescens*
13b. Envés de la hoja pubescente, con los tricomas uniformemente distribuidos sobre la lámina, no concentrados en las axilas de las nervaduras o a lo largo de las mismas.
16a. Ramillas densamente pubescentes.
17a. Arbustos rizomatosos de 0.40–2.50 m de alto; hojas comunmente de 2–4.5 cm de largo; cúpula del fruto de 7–13 mm diám .... 2. *Q. frutex*
17b. Árboles pequeños de 2–7 m de alto; hojas comunmente de 4–7.5 cm de largo; cúpula del fruto de 14–17 mm diám .... 1. *Q. deserticola*
16b. Ramillas glabras o glabrescentes.
18a. Tricomas del envés de las hojas estipitados.
19a. Envés de las hojas con indumento amarillo; frutos sésiles o en pedúnculos de 1–2 mm de largo .... 17. *Q. dysophylla*
19b. Envés de las hojas con indumento blanquecino; frutos en pedúnculos de 3.5–4.0 cm de largo .... 8. *Q. peduncularis*
18b. Pubescencia del envés formada por tricomas sésiles o con un estípite corto.
20a. Tricomas sésiles .... 6. *Q. magnoliifolia*
20b. Tricomas con un estípite corto.
21a. Epidermis del envés de las hojas con algunos tricomas glandulares .... 5. *Q. laeta*
21b. Epidermis del envés de las hojas con abundantes tricomas glandulares.
22a. Margen de la hoja con mucrones de hasta 2 mm de largo; bellota ovoide o angostamente elíptica .... 9. *Q. rugosa*
22b. Margen de la hoja con mucrones cortos, menores de 1 mm, que se curvan hacia el envés; bellota globosa o cilíndrico-ovoide .... 7. *Q. obtusata*
12b. Hojas con borde aristado.
23a. Envés de la hoja glabro, o con tricomas concentrados en las axilas de las nervaduras o a lo largo de las mismas.
24a. Epidermis papilosa, yemas de 1.5–4 mm de largo; árboles altos, de hasta 30 m, crecen en altitudes de 2240–3150 m .... 20. *Q. laurina*
24b. Epidermis no papilosa; yemas de 4–6 mm de largo; árboles bajos, de hasta 12 m de alto, crecen en altitudes menores de 2200 m .... 11. *Q. acutifolia*
23b. Envés de la hoja con los tricomas uniformemente distribuidos sobre la lámina, no concentrados en las axilas de las nervaduras o a lo largo de las mismas.
25a. Envés de las hojas blanquecino, indumento formado por tricomas sésiles.
26a. Hojas con el haz verde lustroso, de 8–14 nervaduras en cada lado; yemas de 3–5 mm de largo; estípulas de 10–15 mm de largo; frutos de 20 mm de largo y de 17 mm de ancho .... 12. *Q. candicans*
26b. Hojas con el haz verde grisáceo, no lustroso, de 5–9 nervaduras en cada lado; pecíolo de 1–4 cm de largo; estípulas de hasta 5 mm de largo; frutos de 8–10 mm de largo y de 10 mm de ancho .... 22. *Q. scytophylla*
25b. Envés de las hojas no blanquecino, indumento formado por tricomas estipitados.
27a. Envés de las hojas con indumento grisáceo; hojas elípticas, elíptico-oblongas, oblanceoladas o lanceoladas .... 13. *Q. castanea*
27b. Envés de las hojas con indumento amarillento: hojas obovadas, oblongo-obovadas, suborbiculares u orbiculares, ovado-elípticas, raramente elípticas.
28a. Ramillas de 5–11 mm diám., hojas panduriformes, suborbiculares, orbiculares, obovado-elípticas u ovadas, de 15–30 cm de largo y de 17–34 cm de ancho .... 23. *Q. urbanii*
28b. Ramillas de 2–5 mm diám., hojas planas, lanceoladas, ovado lanceoladas, obovadas, oblongo-obovadas o elípticas, de 4–20 cm de largo y de 3–12 cm de ancho.

29a. Epidermis de la hoja ampulosa; cúpula del fruto hemisférica; bellota ovoide .... 15. *Q. crassifolia*
29b. Epidermis de la hoja lisa; cúpula del fruto poculiforme a pateliforme; bellota globosa a comprimida .... 19. *Q. hintonii*

1. Quercus deserticola Trelease, Mem. Natl. Acad. Sci. 20: 79, pl. 113. 1924. TIPO: México. Desierto, *Uhde 309* (B).

Quercus alveolata Trel., Mem. Natl. Acad. Sci. 20: 80, pl. 114. 1924. TIPO: Cerro del Gavilán, Puebla, *Purpus 4091* (NY).
Quercus texcocana Trel., Mem. Natl. Acad. Sci. 20: 81, pl. 117. 1924. TIPO: Cerro Texcotsingo, cerca de Texcoco, *Endlich 653* (B).

Arbolillo de 2–7 m de alto, corteza gris; ramillas de 1–3 mm diám., densamente pubescentes, verde-amarillentas, el indumento se ennegrece con el tiempo, formado por tricomas estrellados; lenticelas de hasta 1 mm, blancas, visibles sólo en ramillas viejas; yemas de 2–3.5 mm de largo, ovoides, escamas escariosas con los bordes ciliados; estípulas de 3–5 mm de largo, lineares o filiformes, pilosas, rojizas, persistentes en hojas jóvenes y yemas; hojas jóvenes rojizas, haz verde, con el indumento formado por abundantes tricomas estrellados cortos, estipitados, envés más pálidos, con pubescencia más densa formada también por tricomas estrellados estipitados, pero con las ramas más largas; hojas maduras oblongas, elípticas, elíptico-oblongas u obovadas, subcoriáceas, lámina (2.5–)4–7.5(–8.5) × (1.3–)2–3.5(–4.5) cm, ápice agudo u obtuso, mucronado, base cordada o subcordada, borde entero, revoluto, ondulado o dentado, 2 a 5 dientes mucronados de cada lado, frecuentemente asimétricos; nervaduras de 6 a 9 de cada lado, que se continúan en el diente; haz verde lustroso con tricomas estrellados cortos, estipitados, uniformemente distribuídos, más abundantes en la nervadura central, nervaduras impresas; envés pálido, con abundantes tricomas estrellados, estipitados, con las ramas más largas que los del haz y tricomas glandulares rojizos sobre la epidermis ampulosa y papilosa, nervaduras elevadas; pecíolos de 2–5(–6) mm de largo, de 0.5–1 mm diám., pubescentes al igual que las ramillas, base engrosada; amentos femeninos con 3 a 10 flores en pedúnculos de hasta 30 mm, densamente pubescentes; fruto anual, solitario o en grupos de 2 o 3 sobre pedúnculos de 2–9 mm de largo; cúpula hemisférica, de 14–17(–20) mm diám., las escamas con pubescencia blanca, las de la base engrosadas, las superiores menos pubescentes, ápices obtusos, ligeramente elevados; bellota ovoide, pared interna del pericarpo glabra, de 11–13(–19) mm de largo, de 11–15 mm diám., un tercio de su largo incluida en la cúpula. Figura 1.

Reconocimiento. Quercus deserticola se reconoce por ser un arbolito con las ramillas densamente pubescentes y hojas de hasta 7.5 cm de largo con bordes revolutos y sin aristas.

Distribución y hábitat. En México en los estados de Distrito Federal, Guanajuato, Hidalgo, Jalisco, Estado de México, Michoacán y Querétaro. En bosque de *Quercus*, pastizal y matorral xerófilo, se asocia con *Alnus* y *Cupressus*, en altitudes de 2600–2800 m.

Fenología. Florece en abril y fructifica de julio a diciembre.

Nombres populares y usos. Encino, encino tocuz, encino chico.

Su corteza se usa para curar encías, amacizar los dientes y en curtiduría; su madera como leña, para fabricar pulpa para papel, carbón, postes para cerca, arados, cabos para herramientas y horcones (González, 1986; Bello & Labat, 1987).

Ejemplares examinados. MÉXICO. **Estado de México**: Aculco de Espinosa, San Luis Aculco, *Capse 99* (ENCB); Atizapán, Ciudad Adolfo López Mateos y cercanías, *Matuda 28314* (MEXU); parte alta del Cerro Chiluca, cerca de Ciudad Adolfo López Mateos, *Rzedowski 32588* (ENCB); Coyotepec, Sierra de Alcaparrosa, *Fernández s.n.* (IZTA); Sierra de Alcaparrosa, *Gallardo 1, 2* (IZTA); Sierra de Alcaparrosa, *Romero 153* (IZTA); Ecatepec de Morelos, 6 km al E de San Cristóbal Ecatepec, *Rzedowski 32154* (ENCB); Huixquilucan, cerca de la Presa El Capulín, Fraccionamiento La Herradura, *Rzedowski 25875* (ENCB); Dos Ríos, *Rzedowski 35586* (ENCB); Ixtapaluca, parte alta del Cerro del Pino, *Rzedowski 29655* (ENCB); Teoloyucan, Sierra de Alcaparrosa, *Núñez 1718* (IZTA); Tepotzotlán, Tepotzotlán, *Méndez 30* (ENCB); Sierra de Alcaparrosa, *Núñez 2185* (IZTA); parte baja de la Sierra de Alcaparrosa, 2 km al NNW de Tepotzotlán, *Rzedowski 29912* (ENCB); parte alta de la Sierra de Alcaparrosa, cerca de la estación de microondas, *Rzedowski 29940* (ENCB); Texcoco, Cerro de Tetzcultzingo, 8 km al E de Texcoco, *Pulido 305* (CHAPA, ENCB); Cerro de Tetzcultzingo, *Rzedowski 31790* (ENCB); Timilpan, Sierra de San Andrés, *Camacho 362, 381* (IZTA); Villa del Carbón, Cañón E de la Presa Taxhimay, *Rojas & Romero 3315* (IZTA).

2. Quercus frutex Trelease, Mem. Natl. Acad. Sci. 20: 82, pl. 120. 1924. TIPO: México. México: *Bourgeau 68* (?).

Arbusto rizomatoso de 0.40–2.50 m de alto, a veces es un árbol de hasta 7 m de alto; corteza conformada por escamas cuadrangulares, de color gris opaco; ramillas de 1–1.5 mm diám., densamente pubescentes, pubescencia persistente, for-

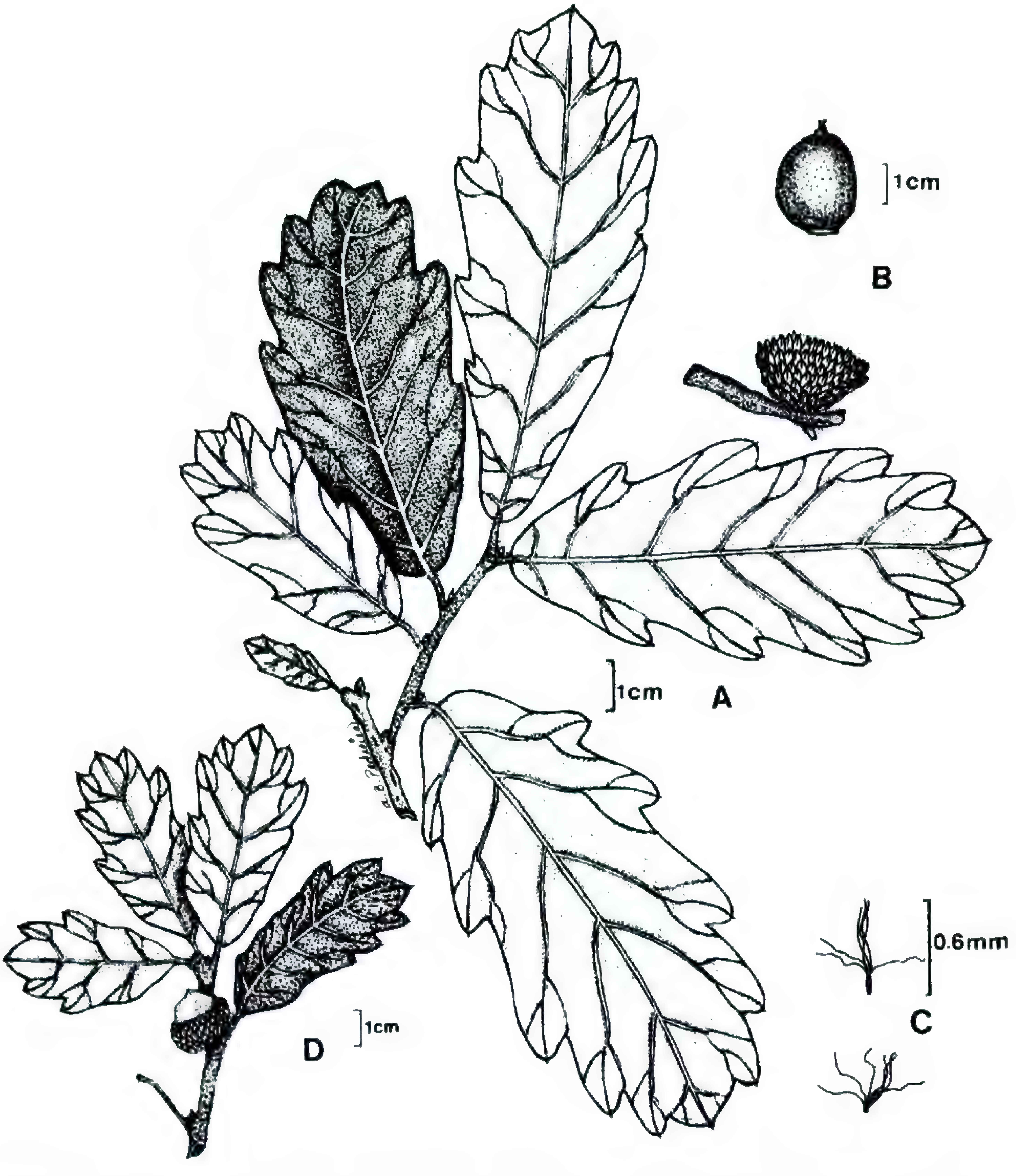

Figura 1. *Quercus deserticola*.—A. Rama. —B. Fruto. —C. Tricomas. —D. Rama. (A–C: *Núñez 1663*; D: *Camacho 379*.)

mada por pelos estrellados, de color amarillento a grisáceo; lenticelas blancas, de hasta 1 mm de largo, a veces protuberantes y entonces muy evidentes a través de la pubescencia, yemas esféricas a ovoides, de 1–3 mm de largo, con escamas pilosas en los bordes; estípulas lineares, de 3–5 mm de largo, pilosas principalmente en la base y en el ápice, glabrescentes con la edad, con frecuencia en las hojas maduras; hojas maduras subcoriáceas, elíptico-oblongas, ovado-lanceoladas u oblanceoladas, lámina (1.5–)2–4.5(–6) × (0.5–)1–2(–2.9) cm, ápice redondeado o agudo, mucronado, base redondeada o subcordada, borde entero, ondulado o con 2 a 4 dientes en las ⅔ partes superiores, revoluto; nervaduras primarias de 6 a 11 en cada lado; haz lustroso, con pelos estrellados dispersos, abundantes en la nervadura central cerca del pecíolo, nervaduras impresas; envés amarillento, pubescente, indumento formado por pelos estrellados estipitados, con rayos largos extendidos que dejan ver la epidermis ligeramente ampulosa y densamente pilosa; nervaduras elevadas; pecíolos de 1–4 × 0.5–1 mm, pubescentes; amentos masculinos de hasta 1.5 cm de largo, raquis densamente pubescentes;

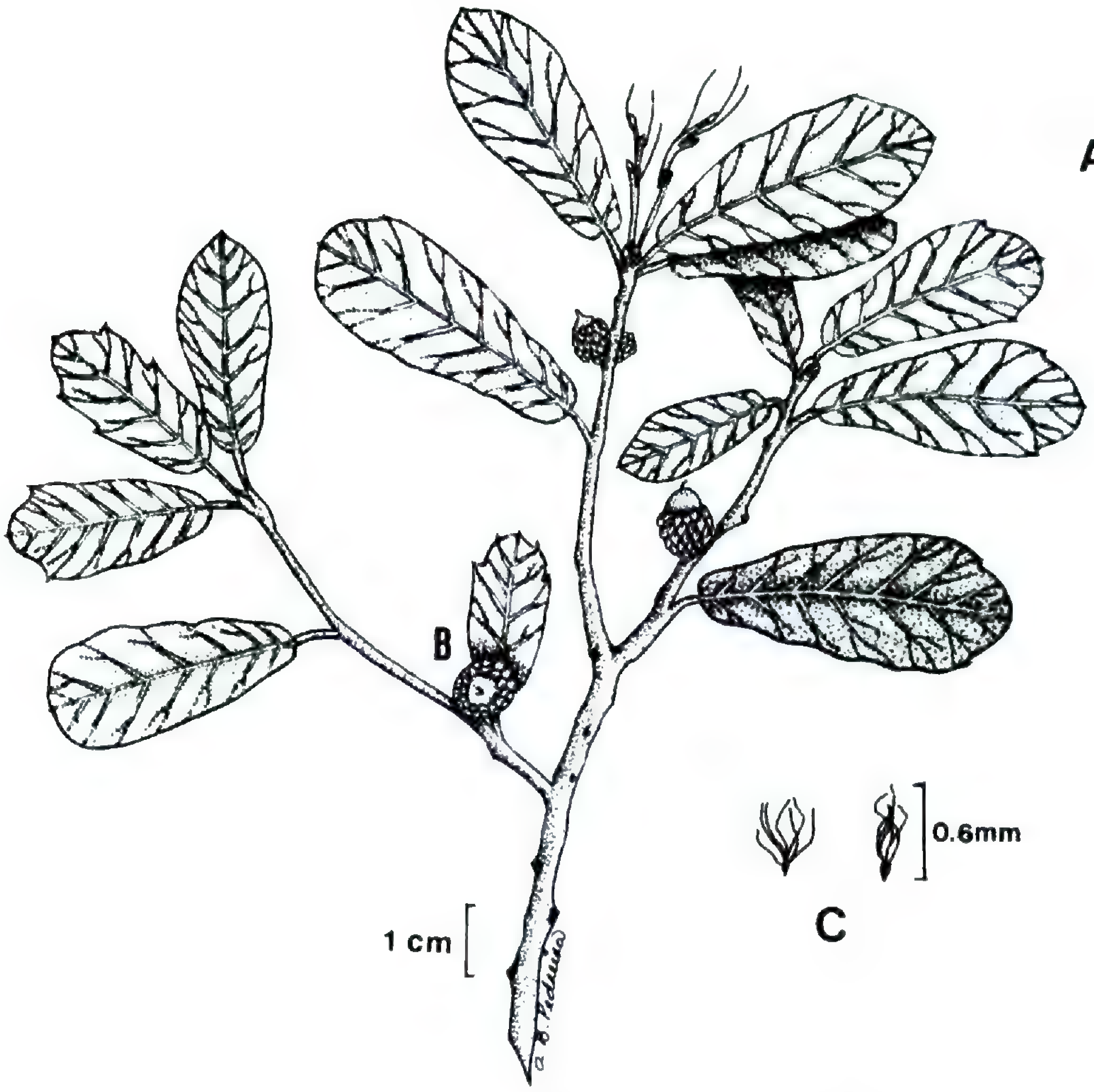

Figura 2. *Quercus frutex.*—A. Rama. —B. Fruto. —C. Tricomas. (*Román 622.*)

perianto sésil, de 2 mm diám., lóbulos ciliados; anteras oblongas de 1 mm de largo, filamentos de 1.5 mm de largo; fruto solitario o en pares, sobre un pedúnculo de 3–10 mm de largo; cúpula hemisférica de 7–13 mm diám., con escamas triangulares, pubescentes, excepto en el dorso superior, engrosadas en la base; bellota ovoide, pared interna del pericarpo glabra, de 5–11 mm diám., incluída ⅓ de su largo en la cúpula. Figura 2.

Reconocimiento. *Quercus frutex* se reconoce por ser un arbusto rizomatoso, con ramillas densamente pubescentes y hojas pequeñas con el ápice mucronado y bordes sin aristas. Puede confundirse con *Q. microphylla*; por ello es que otros autores la han considerado existente en el Estado de México. Se distinguen porque *Q. microphylla* posee el envés de las hojas con pelos estrellados sésiles y *Q. frutex* los presenta estipitados.

Distribución y hábitat. En México en los estados de Jalisco, Hidalgo, Estado de México, Michoacán y Tlaxcala. Se le encuentra en bosques de *Quercus*, pastizal y formando manchones densos en matorral xerófilo y pastizal. Se asocia con *Pinus*, *Juniperus*, *Cupressus* y *Alnus*; también se le encuentra en vegetación perturbada, en altitudes de 2360–3000 m.

Fenología. Florece en junio y fructifica de julio a septiembre.

Nombres populares y usos. Encino, encino compasillo, encino chaparro.

Bello y Labat (1987) mencionan que se utiliza para postes de cercas y como leña.

Ejemplares examinados. MÉXICO. **Estado de México**: Atizapán, 3 km al NW de Ciudad Adolfo López Mateos, *Cruz 620* (ENCB); 4 km al N de Ciudad Adolfo López Mateos, *López 19* (ENCB); Ciudad Adolfo López Mateos y cercanías, *Matuda 28317* (CODAGEM); Coacalco, 6 km al S de Coacalco, *Rzedowski 30776* (ENCB); Ecatepec de Morelos, Sierra de Guadalupe, al N de Coatepec, *Rzedowski 15715* (ENCB); Coyotepec, Sierra de Alcaparrosa, *Gallardo 3, 4* (IZTA); Chalco, Tlachayote, *A. Ventura 3016* (ENCB); El Oro de Hidalgo, Bassoco, *Rojas & Romero 3327* (IZTA); Huehuetoca, ladera Suroeste del cerro Sincoque, *Rojas & Romero 479* (IZTA); ladera E del cerro Sincoque, *Rojas & Romero 700, 701, 1623* (IZTA); Huixquilucan, alrededores de Dos Ríos, *Román 326* (ENCB); Fraccionamiento La Herradura, *Rzedowski 25143* (ENCB); Ixtapaluca, 2 km al E de la Colonia Agrícola Ávila Camacho, *Rzedowski 37294* (ENCB); Naucalpan de Juárez, Villa Alpina, *Rzedowski 32554* (ENCB); Otumba de Gómez Farías, Cerro Cuixi, Santa Bárbara, *Rzedowski 16884* (ENCB); Teotihuacán, Cerro Patlachique, *Chavelas ES-1796* (ENCB); San Martín de las Pirámides, ladera N de Cerro Gordo, *Castilla & Tejero 388* (IZTA); Tenango de Tepopula, Rancho San Luis Aculco, *Hinton s.n.* (ENCB); Tepetlaoxtoc, La Venta, *Ventura 678* (ENCB); Tepotzotlán,

Sierra de la Muerta (Sierra de Alcaparrosa), al NW de Tepotzotlán, *Lot & Wendt 143* (CODAGEM); Parte baja del Cerro de la Cruz, *Rzedowski 33270* (ENCB); Cerro de la Cruz, 6 km al N de Tepotzotlán, *Rzedowski 37055* (ENCB); Texcoco, 20 km al NE de Texcoco, *Cruz 1845* (ENCB); 17 km al E de Texcoco, *Charles & Janice Perina 3397* (CHAPA); 15 km al E de Texcoco, *Muller 9337* (ENCB); Cerro Tetzcultzingo, 7 km al E de Texcoco, *Pulido s.n. 466* (ENCB, MEXU); San Pablo Ixayoc, *Ventura 845* (ENCB); Villa del Carbón, Cañón E de la Presa Taxhimay, *Rojas & Romero 3312* (IZTA); Villa Nicolás Romero, S de la Presa del Consuelo, La Colmena, *Quintero 28* (IZTA); 1 km al N de Magú, *Rzedowski 16850* (ENCB); 2 km al NW de Cahuacán, *Rzedowski 33759* (ENCB); Zumpango, 7 km al N de Zumpango, *Hernández s.n.* (ENCB).

3. Quercus glabrescens Bentham, Pl. Hartw. 56: 348. 1840. TIPO: México. Hidalgo: *Hartweg 428* (B).

Árbol de 10–15 m de alto; ramillas de 1–2.5 mm diám. con lenticelas de color claro, de hasta 1 mm; yemas ovoides de 2.5–3 mm de largo, escamas ovadas con margen ciliado; estípulas oblanceoladas, de 7 mm de largo, glabrescentes, escariosas, persistentes en las yemas; hojas maduras subcoriáceas a coriáceas, oblanceoladas, elípticas u obovadas, lámina (3.5–)4–11 × (1.2–)1.7–4(–5.3) cm, ápice agudo, base redondeada, borde revoluto, cartilaginoso, ondulado o con 3 a 5 dientes mucronados a cada lado en la mitad superior de la hoja, mucrones de hasta 1 mm de largo; nervaduras primarias de 10 a 14 en cada lado, ascendentes, casi rectas, las superiores pasan directamente a formar los mucrones; haz de color verde obscuro contrastando con el envés verde más claro, glabrescente, con pelos glandulares simples sobre las nervaduras y pelos estrellados sésiles, nervaduras impresas; envés glabro o con pelos estrellados sésiles o con un estípite muy corto, ásperos, sobre la nervadura principal, epidermis lustrosa, lisa a papilosa, a veces ligeramente ampulosa, nervaduras elevadas; pecíolos de 3–10 mm de largo, de 0.5–1 mm diám., con indumento formado por pelos estrellados sésiles y ásperos; amentos masculinos de 2 cm de largo, perianto de 2 mm diám., lóbulos ciliados; amentos femeninos de hasta 3 flores, de 1–1.8 cm de largo, raquis glabrescente; frutos solitarios o en grupos de 2 a 3, sésiles o sobre un pedúnculo 4–5 mm de largo; cúpula hemisférica, de 1.3–1.7 cm diám., con las escamas pubescentes, las superiores adpresas, ápice agudo o redondeado, bases engrosadas; bellota ovoide, pared interna del pericarpo glabra, de 1.5–1.8 cm de largo, de 1.2–1.3 cm diám., incluída en la cúpula un tercio de su largo. Figura 3.

Reconocimiento. *Quercus glabrescens* se reconoce porque sus ramillas y el envés de las hojas poseen escasa pubescencia, y porque el borde de ésta tiene dientes mucronados ubicados en la parte apical.

Distribución y hábitat. En México en los estados de Distrito Federal, Hidalgo, Estado de México, Oaxaca, San Luis Potosí, Tlaxcala y Veracruz. En bosque de *Pinus*, *Pinus–Quercus* y en bosque mesófilo de montaña, se asocia con *Alnus*, *Abies*, *Fraxinus*, *Clethra* y *Cornus*, en altitudes de 2450–3000 m.

Fenología. Florece de febrero a junio y fructifica en octubre.

Nombres populares y usos. Encino, encino blanco.

No se conocen usos de esta especie; sin embargo, De la Paz (1985) la recomienda para la elaboración de mangos de herramienta, pisos industriales, cercas, tarimas, construcciones pesadas y para construcciones en general donde se requiera resistencia.

Ejemplares examinados. MÉXICO. **Estado de México**: Amecameca, Barranca cerca de San Antonio Zoyatzingo, *Ern 160* (ENCB); Cerro de Venacho, *Martínez 28078, 28258* (MEXU); Cerro de Venacho, *Matuda 18809, 28072* (CODAGEM); Cerro de Venacho, *Rzedowski 414* (ENCB); abajo de la Joya Alcalica, *Vela & Mancera s.n.* (CHAPA, ENCB, MEXU); Ozumba de Alzate, Techinanco, W del Popocatepetl, *Boyas 576* (MEXU); Texcoco, 2 km al SE de San Pablo Ixayoc, *Rzedowski 24171* (ENCB, MEXU); Cañada al SE de San Pablo Ixayoc, *Rzedowski 32722* (CHAPA, ENCB); Tlalmanalco, 3 km al E de San Rafael, *Barrios 19* (CHAPA, ENCB, MEXU); alrededores de Santo Tomás, *Rzedowski 31890* (CHAPA, ENCB, MEXU); 4 km al E de San Rafael Tlalmanalco, *Rzedowski 32452* (MEXU); base del Iztaccíhuatl, 4 km al SW de San Rafael, *Vera 114* (ENCB); Villa del Carbón, San Jerónimo, *Martínez 39015* (MEXU).

4. Quercus glaucoides M. Martens & Galeotti, Bull. Acad. Roy. Sci. Bruxelles, Vol. 10, pt. 1: 209. 1843. TIPO: México. Oaxaca: *Galeotti 103* (BR).

Árbol de 4–10 m de alto, con el tronco de 25–40 cm diám., corteza gris; ramillas de 1–3 mm diám., de color castaño-rojizo, glabras o pilosas cerca de la base de las yemas, con lenticelas de 0.5–1 mm de largo, protuberantes, pálidas; yemas de 1–2.5 mm de largo, ovoides, obtusas; escamas ciliadas de color castaño, con los bordes papiráceas, ápices obtusos; estípulas de 4–5 mm de largo, lineares, pilosas en los márgenes; hojas jóvenes muy delgadas, no glaucas, haz y envés con abundante pubescencia formada por tricomas estrellados largos, antes de la madurez las hojas son glabras; hojas maduras glabras o con algunos tricomas cerca de la base, glaucas, lámina (8–)10–13(–15) × (3.5–)4–7.5 cm, coriáceas, oblanceoladas, elípticas u obovadas, ápice obtuso,

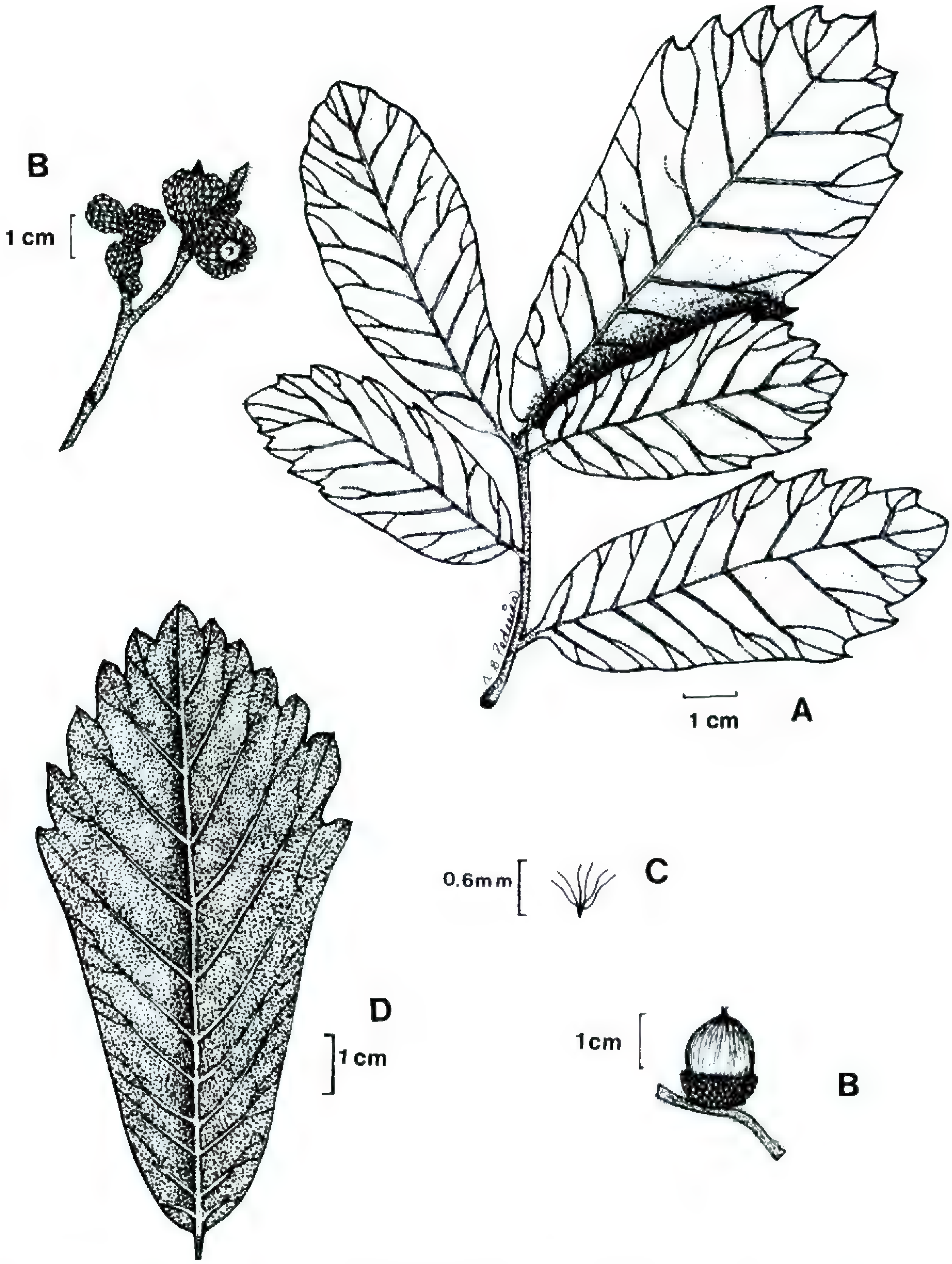

Figura 3. *Quercus glabrescens.*—A. Rama. —B. Fruto. —C. Tricoma. —D. Hoja. (A–C: *Robledo 3*; D: *Chen 2.*)

redondeado o retuso, a veces subagudo, base cordada, redondeada, a veces ligeramente oblicua, borde engrosado, cartilaginoso, plano o ligeramente revoluto, entero, con ondulaciones o con 4 a 7 dientes anchos y obtusos de cada lado; nervaduras de (4)7 a 12 de cada lado, ascendentes, arqueadas o casi rectas, se ramifican cerca del borde de la hoja; haz glabro, de color verde grisáceo, algo lustroso, nervaduras rojizas o amarillentas, la central y primarias ligeramente elevadas; envés glabro o con algunos tricomas cerca de la base, epidermis glauca-cerosa, papilosa, blanquecina, nervaduras elevadas; pecíolos de 2–8 mm de largo, de 1–2 mm diám., de color castaño, rojizo o negro; flores desconocidas; fruto anual, en pares o en grupos de tres, sésiles, o en pedúnculos de hasta 6 cm de largo; cúpula hemisférica, de 9–16 mm diám., escamas adpresas, engrosadas en la base, con abundante pubescencia, ápices triangulares; bellota ovoide, pared interna del pericarpo glabra, de 8–12 mm de largo, de 8–9 mm diám., incluída un tercio de su largo en la cúpula. Figura 4.

Reconocimiento. *Quercus glaucoides* se reco-

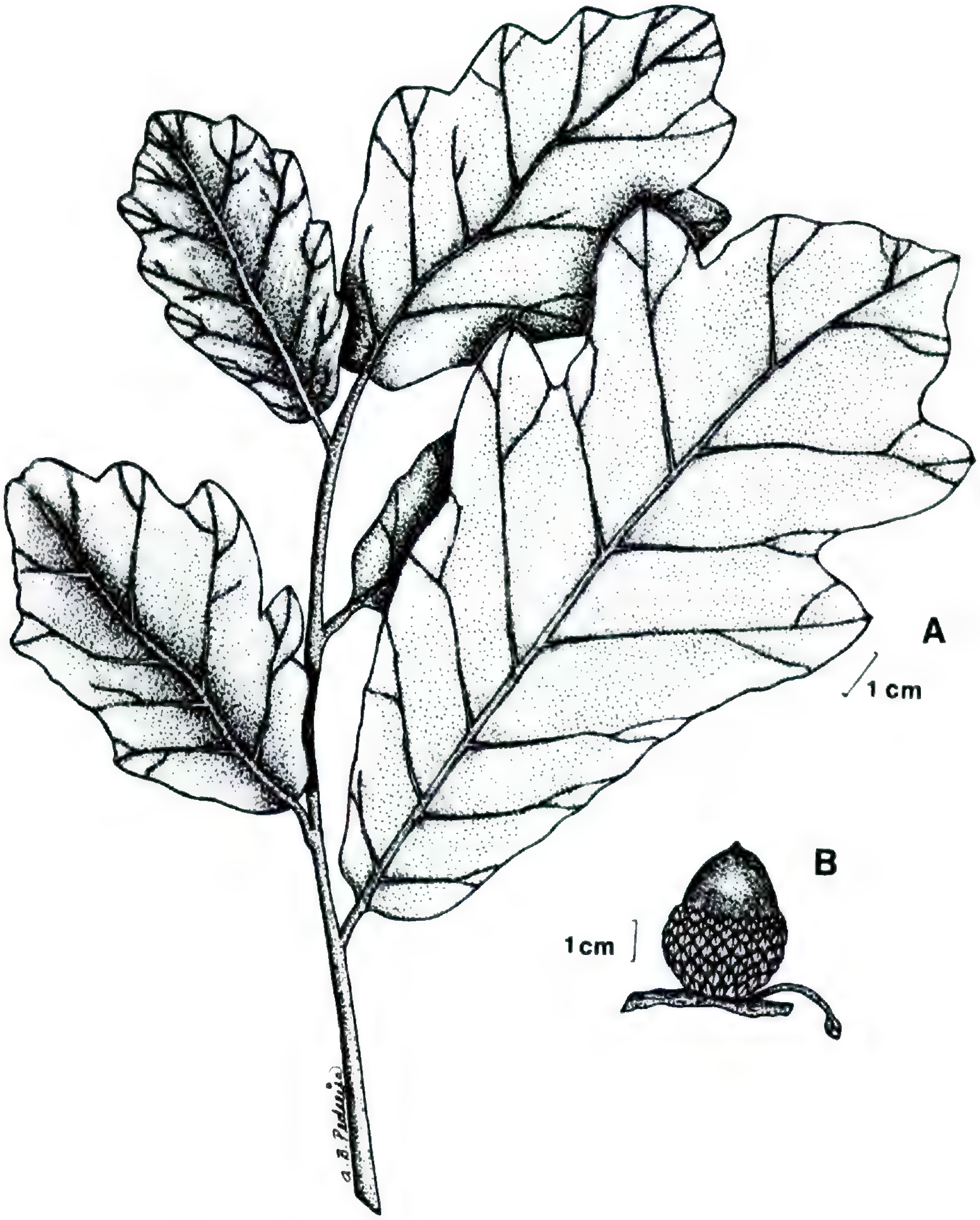

Figura 4. *Quercus glaucoides.*—A. Rama. —B. Fruto. (*Romero 4031.*)

noce por sus hojas de color verde-azuloso con el envés glabro y glauco-acerado. Raras veces, muestra similitud con *Q. obtusata*, debido a que esta última puede presentar el envés de las hojas glauco y casi glabro, y los pecíolos cortos de color obscuro, características muy frecuentes de *Q. glaucoides*; se distinguen porque ésta presenta frutos ovoides, mientras que *Q. obtusata* presenta por lo general, frutos globosos.

Distribución y hábitat. En México en los estados de Jalisco, Michoacán, Estado de México, Guanajuato, Querétaro, Hidalgo, Morelos, Puebla, Guerrero, Oaxaca. En bosque de *Pinus–Quercus*, se le encuentra asociado con *Pinus pringlei*, *Quercus conspersa*, *Q. castanea* y *Q. obtusata*, en altitudes de 750–1800 m.

Fenología. Fructifica de junio a agosto.

Nombres populares y usos. Tocuz, encino blanco, encino negro, encino roble, encino y roble.

Se le usa como leña, para horcones, manufactura de algunos implementos agrícolas y posiblemente por el área de distribución se explote como material celulósico (González, 1986); también se emplea para elaborar carbón, cabos para herramientas, puertas de golpe y postes para cercas (Bello & Labat, 1987). Las hojas y frutos se usan como forraje; las primeras se emplean como medicinales (Vázquez, 1992).

Ejemplares examinados. MÉXICO. **Estado de México**: Ocuilan de Arteaga, 1 km al S de Chalma, *Muller 9220* (MEXU); Santo Tomás de los Plátanos, La Junta, *Martínez 29358* (CODAGEM, MEXU); Sultepec, km 18 carretera Sultepec–San Miguel Totolmoloya, *Torres 384* (IZTA); km 12 carretera Sultepec–San Miguel Totolmolo-

ya, *Torres 388* (IZTA); Tejupilco, Cuadrilla de López, Salto del Agua, *Guízar 6* (MEXU); Mesa de Nanchititla, *Martínez 32801* (MEXU); Nanchititla, *Rodríguez 201* (INIF); Temascaltepec de González, Luvianos, *Breedlove s.n.* (MEXU); Cerro de la Culebra, Luvianos Progreso, *Matuda 31472* (CODAGEM, MEXU); Tlatlaya, Rincón Grande y Llano Tlatlaya, *Martínez 30151* (MEXU); Valle de Bravo, Valle de Bravo, *Boege s.n.* (MEXU); Valle de Bravo, *Martínez 2609* (INIF); Valle de Bravo, *Martínez s.n.* (MEXU); Tiloxtoc, San Bartolo NW de Valle de Bravo, *Muller 9058* (MEXU); Zumpahuacan, cerca de San Gaspar, *Tejero & Castilla 2862* (IZTA).

5. Quercus laeta Liebmann, Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbeider: 179. 1854. TIPO: México. Casa Grande, *Hartweg 419* (B).

Quercus centralis Trel., Mem. Natl. Acad. Sci. 20: 61, pl. 60. 1924. TIPO: México. Distrito Federal: Contreras, *Endlich 1365c* (B).

Árbol de 6–10 m de alto, con el tronco de 25–40 cm diám.; ramillas de 1–2(–3) mm diám., rojizas, glabrescentes, con indumento formado por tricomas estrellados y simples largos, con el tiempo se ennegrece, lenticelas menores de 0.5–1 mm, pálidas, en general no muy abundantes; yemas de 2–4(–5) mm de largo, ovoides, de color castaño, escamas con el dorso pubescente y los bordes ciliados; estípulas 4–6(–7) mm de largo, lineares, pubescentes, persistentes en las yemas apicales; hojas jóvenes de color verde-grisáceo, haz con tricomas estrellados dispersos, más abundantes en la nervadura central, envés muy pubescente, pubescencia formada por tricomas estrellados con sus ramas extendidas; hojas maduras de color verde obscuro, coriáceas, decíduas, elípticas, oblonga-lanceoladas, oblanceoladas u obovadas, lámina 5.5–12(–14) × (2–)3–5.5(–8.5) cm, ápice obtuso o agudo, base redondeada, cordada, a veces cuneada, borde revoluto, engrosado, ondulado o dentado, a veces entero, con 5 a 7 dientes en cada lado, en las dos terceras partes superiores de las hojas, dientes obtusos, con mucrones engrosados y curvos; nervaduras de 7–11(–12) en cada lado, ascendentes, curvas o casi rectas, se prolongan hasta los dientes, y se dividen en la mitad o cerca del borde de la hoja; haz lustroso, glabro o con tricomas estrellados uniformemente distribuidos y tricomas simples en nervadura central, ésta principalmente pubescente en su base, nervaduras impresas, envés pubescente con tricomas estrellados largos, por lo general con sus ramas extendidas, a veces se enredan un poco en su base, estípite corto, tricomas glandulares escasos; epidermis ligeramente ampulosa, papilosa, nervaduras elevadas; pecíolos de (2–)5–10(–13) mm de largo, de 1–2.5 mm diám., pubescentes, ensanchándose en la base; flores desconocidas; fruto anual, solitario o en grupos de 3, en pedúnculos de 1–2.5(–4–7) cm de largo; cúpula hemisférica de 8–11 cm diám., escamas pubescentes, principalmente en la base, ésta engrosada, ápices triangulares, obtusos; bellota ovoide, de 6–13 mm de largo, de 6–7 mm diám., con una tercera parte o la mitad de su largo incluída en la cúpula. Figura 5.

Reconocimiento. *Quercus laeta* se reconoce por sus hojas con el borde mucronado y envés con pubescencia formada por tricomas estrellados con las ramas extendidas y estípite corto. Esta especie muestra similitud con *Q. obtusata* y se distingue porque posee en el envés de las hojas abundantes tricomas glandulares y escasos tricomas estrellados con las ramas enredadas entre sí; además el tamaño de sus hojas es mayor.

Distribución y hábitat. En México en los estados de Aguascalientes, Coahuila, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, Estado de México, Michoacán, Nayarit, Nuevo León, San Luis Potosí, Sinaloa y Zacatecas. En bosque de *Quercus*, bosque de *Pinus–Quercus*, en matorral xerófilo y encinar secundario, se asocia con *Q. obtusata*, *Q. castanea*, *Pinus*, *Abies*, *Cupressus*, *Arbutus*, *Alnus* y *Fraxinus*, en altitudes de 2350–2750 m.

Fenología. Florece en febrero y fructifica de julio a diciembre.

Nombres populares y usos. Encino colorado.

Su madera resulta difícil de trabajar, aunque se usa para la elaboración de algunas herramientas; mas no se considera buena para la elaboración de muebles. También se utiliza como leña, carbón postería, horcones, cercas y como material celulósico (González, 1986).

Ejemplares examinados. MÉXICO. **Estado de México**: Atizapán de Zaragoza, parte alta del cerro Chiluca, *Rzedowski 32585* (IZTA); Jilotepec, km 67 carretera Tlalnepantla–Jilotepec, *Cisneros 5* (IZTA); Denhxi, *Martínez 64* (IZTA); Tenango del Valle, Rancho Yeca, *Ávila s.n.* (INF); Tepotzotlán, Sierra de Alcaparrosa, *Núñez 440, 1574* (IZTA); Villa Nicolás Romero, km 8 Carretera Villa Nicolás Romero–Tlazala de Fabela, límite del municipio, *Quintero 36* (IZTA); km 28 carretera Tlalnepantla–Villa del Carbón, *Rojas & Romero 3165* (IZTA); Barrio IV, *Rojas & Romero 3192* (IZTA).

6. Quercus magnoliifolia Née, Anales Ci. Nat. 3: 268. 1801 (como *magnoliaefolia*). TIPO: México. Guerrero: entre Chilpancingo y Tixtla, *Née s.n.* (MA).

Quercus macrophylla Née, Anales Ci. Nat. 3: 274. 1801. TIPO: Entre Chilpancingo y Tixtla, *Née s.n.* (MA).
Quercus platyphylla E. F. Warb., Bull. Misc. Inform.: 85. 1939. TIPO: México. Estado de México: *Hinton 6360* (K).

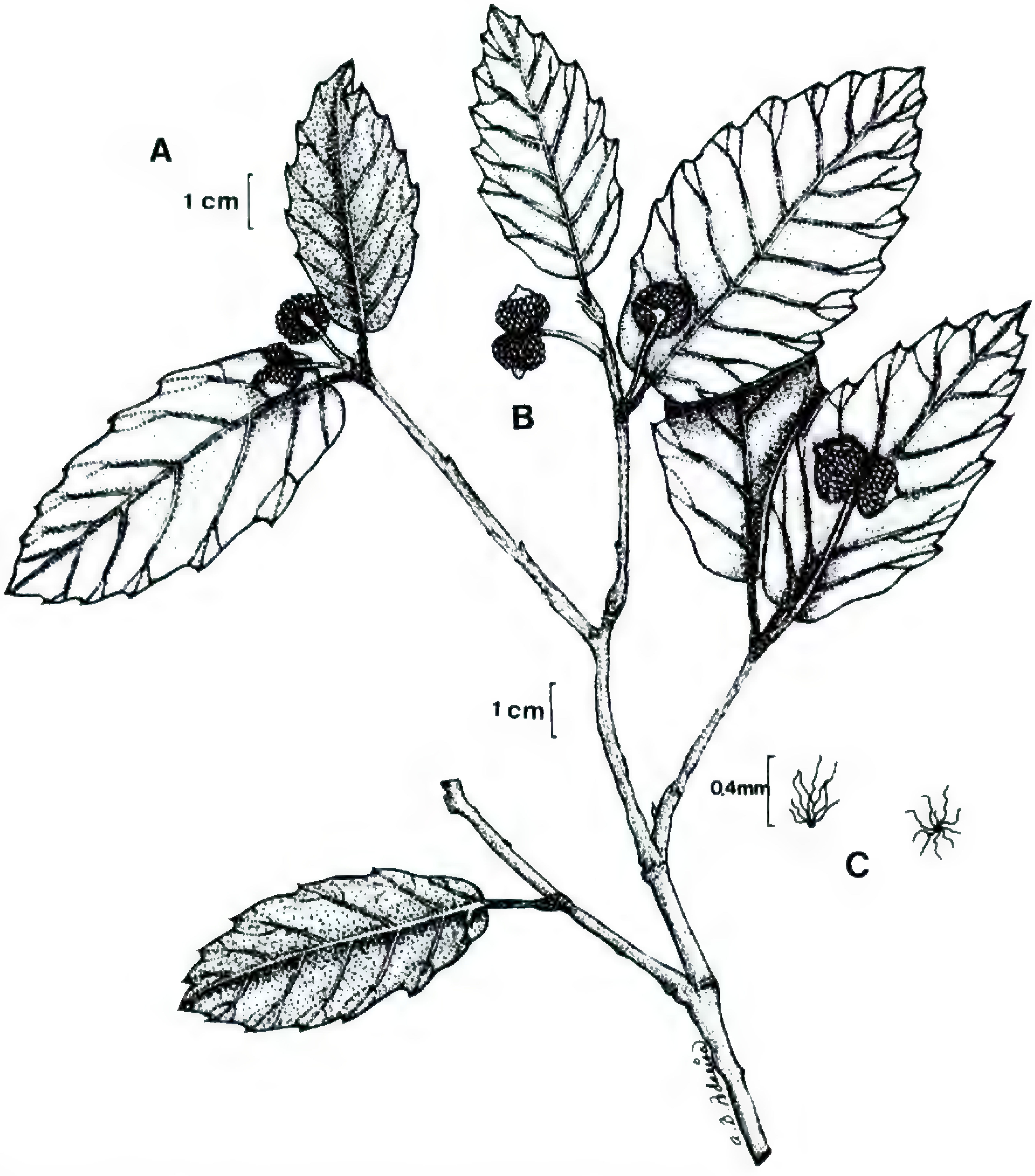

Figura 5. *Quercus laeta*.—A. Rama. —B. Fruto. —C. Tricomas. (*Urbina 4*.)

Árbol de 3–15 m de alto, tronco de 20–50 cm diám.; ramillas de 2–4 mm diám., glabrescentes, con tricomas estrellados y glandulares cortos, éstos de color ámbar-rojizo; lenticelas muy notorias, pálidas, menores de 0.5–1.5 mm de largo; yemas de 1.5–5 mm de largo, ovoides, de color castaño, gruesas, pubescentes, principalmente en los márgenes; estípulas filiformes, de 2–10 mm de largo, pubescentes; hojas jóvenes rojizas por la abundancia de tricomas glandulares, con tricomas estrellados muy cortos, dispersos; envés más pálido; hojas maduras, por lo general obovadas o elípticas, lámina (7–)10–27(–32) × 6–12.5(–21) cm, ápice obtuso, redondeado o agudo, base atenuada, cuneada, redondeada o auriculada, borde engrosado, ligeramente revoluto, sinuado, dentado o sinuado-dentado, dientes 8 a 14 en cada lado, con un mucrón corto y doblado en el ápice de cada diente u ondulación; nervaduras primarias 11 a 20 en cada lado, ascendentes, rectas o ligeramente curvadas, pasan directamente a formar los mucrones, a veces nervaduras secundarias los forman; haz verde lustroso, glabro, con tricomas estrellados y glandulares en la base de la nervadura central, nervaduras impresas, las secundarias y más pequeñas poco notorias; envés verde-amarillento, más claro que el haz, con pubescencia abundante o escasa, formada de tricomas glandulares y estrellados sésiles muy cortos, adpresos a la epidermis, ésta ampulosa y papilosa, nervaduras elevadas; pecíolos de 5–10 × 1–4 mm, más anchos de la base, pubescentes, principalmente por el envés de las hojas; amentos masculinos con numerosas flores, de 6–10 cm de largo, perianto membranoso, largamente ciliado, de 3–4 mm

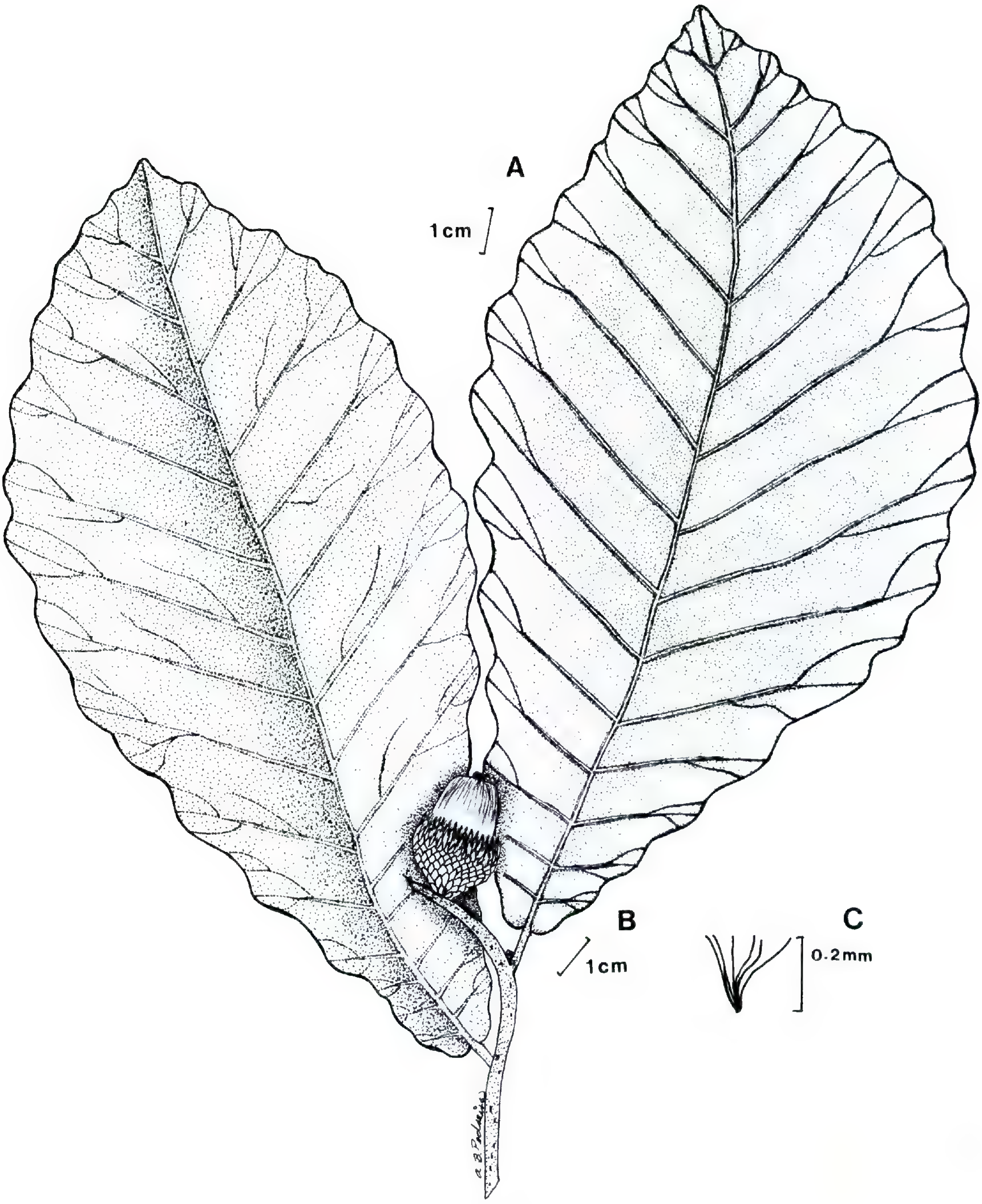

Figura 6. *Quercus magnoliifolia*.—A. Rama. —B. Fruto. —C. Tricoma. (*Soto 283*.)

diám., anteras de 10 a 12, de 1–1.5 mm de largo; flores femeninas solitarias, en grupos de 2 o 3 ó más, dispersas sobre un pedúnculo de 5–10 cm de largo, fruto anual, la cúpula de 14–25 cm diám., escamas obtusas pubescentes, engrosadas en su dorso, ápice más delgado, angostamente triangular; bellota ovoide, pared interna del pericarpo glabra, de 8–22 mm de largo, de 7–15 mm diám., arrugadas cuando maduras, de una a dos terceras partes de su largo incluída en la cúpula. Figura 6.

Reconocimiento. *Quercus magnoliifolia* se reconoce por sus hojas generalmente grandes, obovadas o casi elípticas, con mucrones, haz verde lustroso y nervaduras casi rectas.

Distribución y hábitat. En México en los esta-

dos de Colima, Guerrero, Jalisco, Estado de México, Michoacán, Nayarit, Oaxaca y Sinaloa. En bosque de *Pinus*, *Quercus* y *Pinus–Quercus*, se asocia con *Pinus oocarpa*, *Quercus hintonii* y *Q. elliptica*; se le encuentra también en encinares perturbados, en altitudes de 1700–2600 m.

Fenología. Florece en febrero y fructifica en junio y julio.

Nombres populares y usos. Encino, encino roble, roble, encino amarillo, encino napis, encino prieto, encino blanco, encino bermejo, encino avellano.

Su madera se utiliza como leña, carbón, postería, horcones, para fabricar mangos para herramientas, bancos, vigas, postes para corral y para extraer celulosa. Su follaje sirve para fabricar techos rústicos de viviendas del campo y sus frutos como forraje para cerdos (González, 1986; Bello & Labat, 1987; Vázquez, 1992).

Ejemplares examinados. MÉXICO. **Estado de México**: Amatepec, Amatepec y cercanías, *Matuda 29822* (CODAGEM); Clachichilpan, 7 km al NE de Amatepec, *Pineda 1049* (INIF); Las Trojas, *Rodríguez 185* (INIF); Ixtapan del Oro, cerro ubicado al SW de la presa Tiloxtoc, *Estrada 850* (INIF); Cerro el Cualtenco, al E de la laguna de Valle de Bravo, *Estrada 852* (INIF); Ocuilan de Arteaga de Arteaga, cerro la Llovizna, *Nah 1179* (INIF); Nuevo Santo Tomás de los Plátanos, La Junta, *Matuda 29356* (CODAGEM); Sultepec, Las Tinajas, *Rodríguez s.n.* (CHAPA, INIF); km 12 carretera Sultepec–San Miguel Totolmoloya, *Torres 90, 110, 194* (IZTA); km 18 carretera Sultepec–Salayatla, *Torres 251* (IZTA); Tejupilco, Nanchititla, *Bringas 420* (CODAGEM); Cañada de Nanchititla, *García 454* (CODAGEM, ENCB); Nanchititla, *García s.n.* (INIF); proximidades de Tenería, *Guízar 155* (CHAPA, ENCB); camino de Almoloya de la Granadas, *Guízar 351* (ENCB); Cañada de Nanchititla, *Soto & Moreno 183, 283* (IZTA); Temascaltepec de González, km 70 carretera federal 104, *Figueroa 16* (IZTA); km 65 de la carretera Toluca–Temascaltepec, *Jiménez 5* (IZTA); carretera Toluca–Temascaltepec, *Tejero & Castilla 339* (IZTA); Zacualpan, km 2–3 terracería Campana de Plata a Subestación Coronas, *Castilla & Tejero 1796* (IZTA); km 3–4 carretera Zacualpan–Mamatla, *Fragoso 339* (IZTA).

7. Quercus obtusata Humboldt & Bonpland, Pl. Aequinoct. 2: (26). Pl. 76. 1809. TIPO: México. Michoacán: Ario de Rosales, *Bonpland 4329* (isotipo, B!).

Quercus atringlans Warb., Bull. Misc. Inform.: 88. 1939. TIPO: México. Estado de México: Temascaltepec de González, *Hinton 6549* (K).

Árbol de 6–20 m de alto, tronco de 40–60 cm diám. o más, con la corteza gris, escamosa; ramillas glabrescentes, rojizas a gris o negras, de (1–)2–3 mm diám., indumento formado por tricomas glandulares y estrellados, lenticelas pálidas, de hasta 2 mm de largo; yemas ovoides, de (1.5–)2–4(–5) mm de largo, de color castaño obscuro, escamas pubescentes en los márgenes; estípulas lineares, de 5–8 mm de largo, membranosas, pubescentes; hojas jóvenes con el haz rojizo por la abundancia de los tricomas glandulares, envés amarillento, densamente pubescente, indumento formado por tricomas estrellados entrelazados; hojas maduras decíduas, gruesas y coriáceas, rugulosas, obovadas a largamente obovadas o elípticas, lámina (4–)6–17(–22) × (2–)3–8(–11) cm, ápice obtuso o anchamente redondeado, a veces algo agudo, borde engrosado, revoluto, dentado, sinuado o dentado-sinuado, con 3 a 9 dientes u ondulaciones, que frecuentemente se distribuyen desde el ápice hasta la base de la hoja, cada diente u ondulación termina en un mucrón corto, que se dobla junto con el borde revoluto, nervaduras de 7 a 12 en cada lado, ascendentes, rectas o ligeramente curvas, cada nervadura secundaria pasa a formar un mucrón que coincide con el ápice del diente u ondulación, a veces el mucrón se forma entre ondulaciones; haz verde lustroso, glabrescente, con tricomas simples y estrellados dispersos, más abundantes en la base de la nervadura central, nervaduras primarias impresas o ligeramente protuberantes; envés verde-amarillento, opaco, con pubescencia dispersa formada por tricomas estrellados con estípite muy corto, a veces muy escasos, de aproximadamente 8 rayos, enredados entre sí o algo extendidos, de pocos a abundantes tricomas glandulares color ámbar o rojizos, a veces se forman gotas de exudado, epidermis ligeramente ampulosa y papilosa; pecíolos glabrescentes de (3–)4–11(–15) mm de largo, de 1–2 mm diám., a veces de color obscuro; amentos masculinos de 3 cm de largo, con muchas flores distribuidas a lo largo del raquis, perianto de 2 mm diám., largamente pubescente, 6 estambres, anteras de 1 mm de largo, filamento de 1 mm de largo; amentos femeninos de 3 a 6 o más flores distribuidas en la mitad distal de un pedúnculo de 2–3.5 cm de largo, pubescentes; fruto anual, solitario o en grupos de 2 o 3 ó más, pedúnculos de 1.8–3.5 mm de largo; cúpulas hemisféricas, de poco a muy profundas, de 12–18 mm diám.; escamas muy pubescentes, ápice agudo, bases engrosadas; bellota globosa, a veces cilíndrico-ovoide, con la pared interna del pericarpo glabra, de 6–20 mm de largo, de 11–19 mm diám., hasta un tercio de su largo incluída en la cúpula. Figura 7.

Reconocimiento. *Quercus obtusata* se reconoce por sus hojas obovadas, con mucrones robustos que se doblan hacia el envés, éste con abundantes tricomas glandulares y escasos tricomas estrellados con las ramas enredadas entre sí; las bellotas son globosas. *Quercus obtusata* muestra similitud con

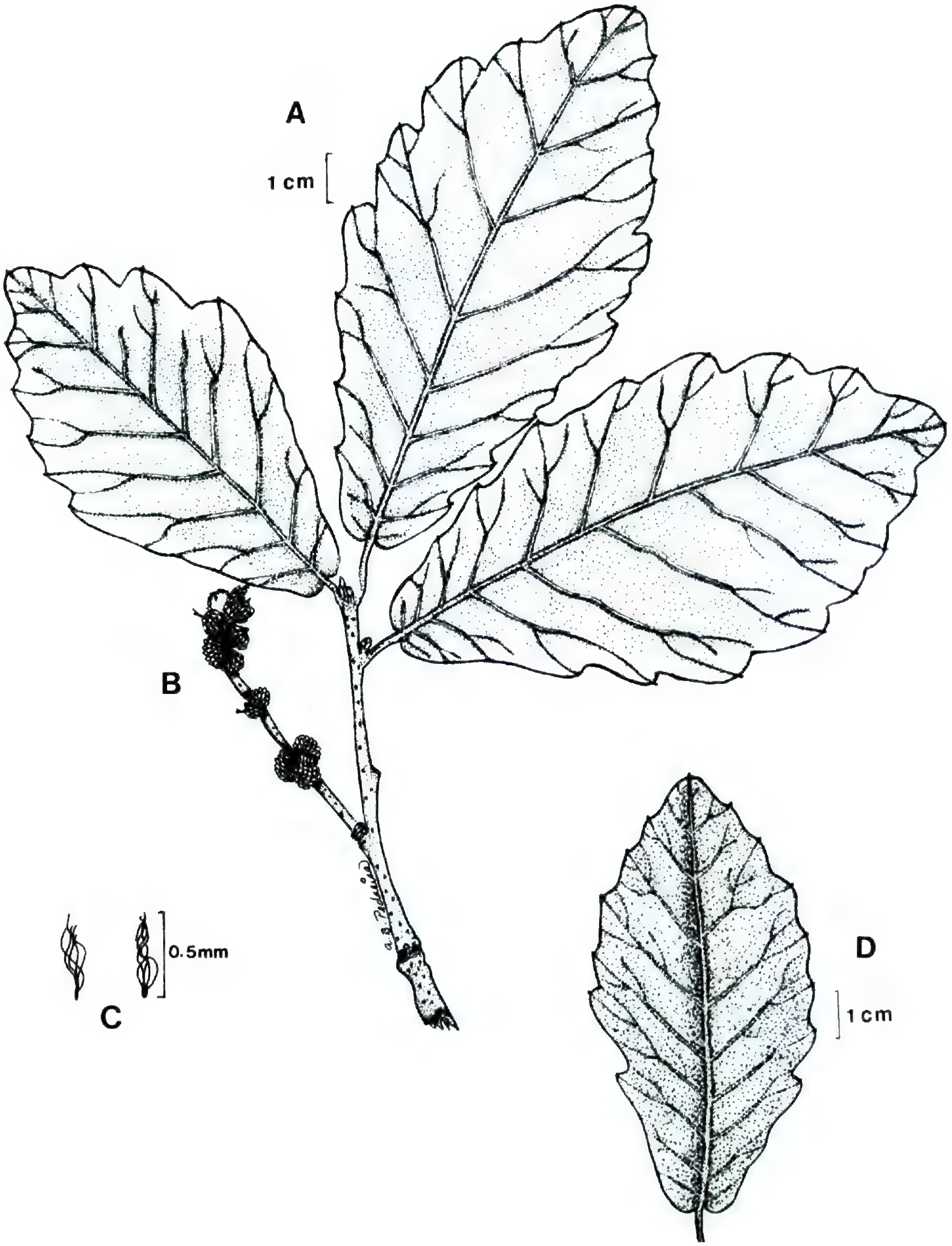

Figura 7. *Quercus obtusata.*—A. Rama. —B. Frutos. —C. Tricomas. —D. Hoja. (*Torres 195.*)

Q. laeta la cual se reconoce por sus hojas con el borde mucronado y envés con pubescencia formada por escasos tricomas glandulares y abundantes tricomas estrellados con las ramas extendidas y estípite corto.

Distribución y hábitat. En México en los estados de Guanajuato, Hidalgo, Jalisco, Estado de México, Michoacán, Morelos, Nayarit, Puebla, San Luis Potosí y Zacatecas. En bosques de *Pinus*, *Quercus* y *Pinus–Quercus*, se asocia con *Pinus leiophylla*, *P. montezumae*, *P. michoacana*, *Cupressus*, *Quercus candicans*, *Q. urbanii* y *Q. glaucoides*; también se le encuentra en bosque mesófilo de montaña y pastizal con matorral xerófilo de *Acacia* y *Opuntia*. Es frecuente en encinares perturbados, en altitudes de 1430–2850 m.

Fenología. Florece de abril a mayo y fructifica de agosto a octubre.

Nombres populares y usos. Roble, encino, encino prieto, encino calicahuac, encino negro, encino cosahuicahuatl, encino blanco, encino roble, encino rojo, encino chino, tocuz, uricua, charari.

Se utiliza para leña, carbón, postes para cerca, implementos agrícolas, horcones, cabos para herramienta, curtir pieles; la corteza tiene usos medicinales, y como material de construcción (Bello & Labat, 1987).

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, cerro Hondingá, *Estrada 1443* (IZTA); Almoloya de Alquisiras, San Andrés, *Rodríguez s.n.* (INIF); Coatepec de Harinas, 4 km al E de Coatepec de Harinas, *Martínez 2697, 2840* (INIF); Donato Guerra, El Mirador de Donato Guerra, Toluca–Valle de Bravo, *Rojas & Romero 3242* (IZTA); Ocuilan de Arteaga de Arteaga, Loma de Fuego, *Gutiérrez 403* (INIF); cerro de La Llovizna, *Nah 1180, 1181, 2340* (INIF); Sultepec, Las Trojas, *Rodríguez 162* (INIF); km 12 carretera Sultepec–San Miguel Totolmoloya, *Torres 195* (IZTA); Tejupilco, Nanchititla, *Rodríguez 200* (CHAPA, INIF); Temascaltepec de González, Ypericones, *Hinton 6549* (INIF); Estancia Vieja, 10 km al S de Temascaltepec de González, *Moreno 168* (INIF); Real de Arriba, *Rocha s.n.* (INIF); Tenancingo, Las Cumbres, *Rodríguez 31* (INIF); Las Cumbres, *Rodríguez s.n.* (CHAPA, INIF); Tenango de Tepopula, Rancho San Luis Aculco, *Hinton 17989* (ENCB); Tepozotlán, Cerro de Tres Cabezas, *Madrigal & Vela s.n.* (INIF); Texcoco, 1 km al SE de San Pablo Ixayoc, *Rzedowski 24193* (INIF); Valle de Bravo, 2 km al E de Pipioltepec, *Pineda & Ochoa 1256* (INIF); Godines Tehuastepec, *Rodríguez 205, 206* (INIF); Villa del Carbón, km 28 carretera Tlalnepantla–Villa del Carbón, *Rojas & Romero 3165* (IZTA); Las Golondrinas, a 1000 m del límite con Hidalgo, *Rojas & Romero 3308, 3310* (IZTA); Villa Nicolás Romero, 3 km al W de Cahuacán, *Rzedowski 32631* (INIF); Zacualpan, Subestación Coronas, *Jiménez 13* (IZTA).

8. Quercus peduncularis Née, Anales Ci. Nat. 3: 270. 1801. TIPO: México. Entre México y Acapulco, *Née s.n.* (MA).

Quercus dolichopus E. F. Warb., Bull. Misc. Inform.: 87. 1939. TIPO: México. Estado de México: Temascaltepec de González, *Hinton 6378* (holotipo, K no visto).

Árbol de 4 m de alto; ramillas de 2–2.5 mm diám., glabrescentes, en un principio con un denso tomento formado por tricomas estrellados estipitados con rayos largos; lenticelas visibles sólo en ramillas viejas, de color claro, de hasta 1 mm de largo; yemas de 3–4 mm de largo, ovoides, con las escamas obtusas, ciliadas en los bordes y dorso; estípulas de 5–7 mm de largo, subuladas o lineares, con tomento largo o glabrescente, persistentes aún en las hojas maduras; hojas jóvenes muy delgadas, de color verde obscuro, haz con fina pubescencia formada por tricomas estrellados cortos, algunos largos, envés densamente pubescente, de color claro; hojas maduras subcoriáceas, oblanceoladas, elípticas u obovadas, lámina (4–)7–10 × (2.5–)3–5 cm, ápice obtuso o agudo, base atenuada, redondeada o subcordada, a veces asimétrica, borde cartilaginoso, revoluto, casi siempre dentado, con 7 a 10 dientes mucronados a cada lado, desde la base de la hoja, nervaduras 9 a 14 en cada lado, ascendentes, casi rectas, pasan directamente al diente, se ramifican cerca del borde; haz lustroso, de color verde obscuro, glabro, excepto la base que presenta tricomas estrellados parecidos a los del envés, nervadura central algo convexa, las primeras impresas; envés con indumento blanquecino formado por tricomas estrellados estipitados, los rayos largos y extendidos que se entrecruzan con otros, epidermis ampulosa y papilosa, nervaduras pálidas, convexas; pecíolos de 2–5 mm, pubescentes; flores desconocidas; fruto anual, solitario o en pares sobre pedúnculos de 3.5–4 cm de largo, de 1 mm diám.; cúpula hemisférica de 12–13 mm diám., escamas pubescentes, sus ápices glabrescentes, agudos o acuminados; bellota ovoide, pared interna del pericarpo glabra, de 8–13 mm diám., de uno a dos tercios incluida en la cúpula. Figura 8.

Reconocimiento. *Quercus peduncularis* es una especie muy escasa en la entidad; sin embargo se encuentran comunidades en donde esta especie es abundante. Se reconoce porque el envés de sus hojas es tomentoso y blanquecino y los pedúnculos de los frutos son largos.

Distribución y hábitat. En México en los estados de Colima, Chiapas, Guerrero, Jalisco, Estado de México, Michoacán, Oaxaca y Veracruz, también en América Central. Bosque de *Pinus–Quercus*, se asocia con *Alnus*, en altitudes de 2550 m.

Fenología. Fructifica en julio.

Nombres populares y usos. Encino, roble, encino blanco, encino avellano, encino zopilote negro, mazcahuite.

La madera se emplea como carbón, leña y material celulósico para papel (González, 1986).

Ejemplares examinados. MÉXICO. **Estado de México**: Temascaltepec de González, San Lucas, *Hinton 6376* (INIF); Temascaltepec de González, *Hinton 67331* (MEXU); NE de San Francisco Oxtotilpan, *Orozco 268* (IZTA).

9. Quercus rugosa Née, Anales Ci. Nat. 3: 275. 1801. TIPO: México. Estado de México: Huixquilucan y Ocuilan de Arteaga, *Née s.n.* (MA).

Quercus conglomerata Trel., Mem. Natl. Acad. Sci. 20: 77, pl. 106. 1924. TIPO: México. Michoacán: Tlalpuxahua, *Hartweg 429* (B).

Quercus decipiens Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles, Vol. 10, pt. 1: 214. 1843. Syn. nov. TIPO: México. Mirador, *Galeotti 131* (BR).

Figura 8. *Quercus peduncularis*.—A. Rama. —B. Fruto. —C. Tricomas. (*Hinton 6331*.)

Quercus reticulata Humb. & Bonpl., Pl. Aequinoct. 2: 40(35), pl. 86. 1809. TIPO: México. Guanajuato: Santa Rosa, *Bonpland 4408* (B).

Árbol de (5–)10–30 m de alto, con el tronco de hasta 1 m ó más diám.; ramillas gruesas, de 1.5–4 mm diám., glabrescentes, de color gris-castaño, tricomas del indumento estrellado-estipitados, que se ennegrecen con el tiempo; lenticelas hasta de 1 mm, en las ramas viejas más grandes y protuberantes; yemas de 2–5 mm de largo, ovoides, de color café-rojizo, escamas coriáceas, pubescentes; estípulas lineares u oblanceoladas, decíduas, de 5–7 mm de largo, piloso-sedosas; hojas jóvenes con el haz rojizo y abundantes tricomas glandulares, vena principal muy pubescente, envés con densa pubescencia pálida, epidermis totalmente cubierta de tricomas glandulares amarillentos, nervadura con tricomas glandulares rojizos; hojas maduras decíduas, coriáceas, rígidas, con frecuencia cóncavas, muy rugosas, elípticas, elíptico-obovadas, obovadas o casi suborbiculares, lámina (3.2–)5–15(–19) × 2–8(–10) cm, ápice obtuso, a veces agudo, base redondeada o cordada, borde sinuado o dentado, engrosado, plano o revoluto, dientes de 5 a 12 en cada

lado distribuidos en las ⅔ partes superiores, agudos u obtusos, con mucrón corto hasta de 1–2 mm de largo; nervaduras de 7 a 12 en cada lado, rectas o curvadas, pueden pasar directamente al mucrón o ramificarse antes y las ramificaciones pasar a los mucrones adyacentes; haz algo lustroso, verde o grisáceo, glabro o con pocos tricomas estrellados y tricomas glandulares, principalmente en la nervadura media, nervaduras central, primarias y secundarias impresas, las más finas elevadas formando un retículo pálido; envés densamente pubescente o con tricomas esparcidos; pubescencia formada por tricomas estrellados con un estípite corto, sus rayos enredados, tricomas glandulares vermiformes de color ámbar o rojizos; epidermis ligeramente o marcadamente ampulosa, papilosa; pecíolos pubescentes, de (3–)5–10(–13) mm de largo, de 1–3 mm diám., rojizos; amentos masculinos de 15–20 mm de largo, pubescentes, perianto campanulado, de 2 mm diám., bordes ondulados y largamente ciliados, anteras glabras; amentos femeninos con 15 a 20 flores en pedúnculos pubescentes; fruto anual, solitario o en grupos de 2–5(–8), en pedúnculos de (0.8–)1.5–5(–8) cm de largo; cúpula hemisférica, de 8–15 mm diám., de 6–10 mm de alto, escamas engrosadas en la base, pubescentes en el dorso, de color café rojizo; bellota ovoide o angostamente elíptica, pared interna del pericarpo glabro, ápice agudo de 9–28 mm de largo, de 7–14 mm diám., incluída una tercera o hasta la mitad de su largo. Figura 9.

Reconocimiento. *Quercus rugosa* se reconoce por sus hojas coriáceas y cóncavas, los mucrones largos y envés con tricomas glandulares y depósitos de mucílago. *Quercus rugosa* puede confundirse con *Q. obtusata*; ésta última se distingue por la presencia de mucrones callosos en los márgenes de las hojas, mientras que *Q. rugosa* los presenta prominentes de hasta 2 mm de largo.

Distribución y hábitat. En México en los estados de Aguascalientes, Coahuila, Chihuahua, Distrito Federal, Durango, Guanajuato, Hidalgo, Jalisco, Estado de México, Michoacán, Puebla, Veracruz y Zacatecas. En bosques de *Pinus–Quercus*, de *Pinus*, de *Quercus*, de *Abies*, en matorral xerófilo, en encinares perturbados y cultivos agrícolas; se asocia con *Pinus leiophylla*, *P. oocarpa*, *P. teocote*, *P. pseudostrobus*, *Quercus castanea*, *Q. candicans*, *Q. laurina* y *Q. crassipes*, en altitudes de 1700–3500 m.

Fenología. Florece en agosto y fructifica de septiembre a noviembre.

Nombres populares y usos. Roble, doga, encino, encino roble, encino quebracho, encino hojarasco, encino negro, encino cuero, encino blanco, encino asta, encino avellano, encino miel, encino blanco liso, encino quiebra hacha.

La corteza se utiliza en el tratamiento de la disentería, dolor de muelas, hemorragias y fortalecimiento de los dientes; usada junto con las hojas sirve para preparar la infusión que se utiliza para el tratamiento contra el dolor muscular, la tos (Chino & Jacques, 1986). Se sabe también que las bellotas sirven para elaborar café o pueden consumirse tostadas; también se usan como forraje (Vázquez, 1992). La madera se utiliza para la obtención de papel y como leña (González, 1986).

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, cerro Detiña, *Estrada 1467* (IZTA); Aculco de Espinosa, km 117 carretera a Toluca, *Rojas & Romero 2150* (IZTA); Axapusco, Cerro del Tepayo, Jaltepec, *Ventura 675* (INIF); Amanalco de Becerra, San Jerónimo Amanalco, *Ventura 586* (ENCB); alrededores de Amanalco de Becerra, *Villa 163* (INIF); Amecameca, San Antonio Zoyatzingo, *Ávila s.n.* (INIF); cerro Sacromonte, *Román 409* (IZTA); Atizapán, cerro Chiluca, 16 km al SW de Ciudad Adolfo López Mateos, *Patiño 333* (CHAPA, INIF); Coyotepec, Sierra de Alcaparrosa, *Fernández 134* (IZTA); parte alta de la Sierra de Alcaparrosa, 6 km al W de Coyotepec, *Rzedowski 37251* (ENCB); Chapa de Mota, cercanías del observatorio astronómico, *Rojas & Romero 2796* (IZTA); Donato Guerra, Mirador de Donato Guerra, *Rojas & Romero 3243* (IZTA); Ecatepec de Morelos, Sierra de Guadalupe, *Suárez 11* (IZTA); Ecatzingo, Ecatzingo, *Matuda 29023, 29026, 29029* (CHAPA); El Oro de Hidalgo, La Cima, *Gómez 1* (IZTA); cercanías de El Oro de Hidalgo, *Matuda 28621, 32613* (CODAGEM); Jilotepec, Jilotepec, *Matuda 26668* (CODAGEM); cerro de Jilotepec, *Matuda 27821* (CODAGEM); Llano Grande, 6 km al N de Canalejas, *Rojas & Romero 3142* (IZTA); Santa Ana Jilotzingo, Las Manzanas, *Hernández 13* (IZTA); Jiquipilco, km 21 carretera Naucalpan–Jiquipilco, *Guzmán 10* (IZTA); Ocuilan de Arteaga, Ocuilan de Arteaga, *Martínez 31748* (IZTA); cerro de La Llovizna, *Nah AM-5* (INIF); Otumba de Gómez Farías, Ranchería Buenavista, 8 km al E de San Marcos, *Fuentes AIII-32 y AIII-33* (MEXU); San Martín de las Pirámides, cerro Gordo, *Castilla & Tejero s.n.* (ENCB); Sultepec, Real de Abajo, *Matuda 29186* (CHAPA); Las Trojes, *Rodríguez 180* (INIF); Temascalapa, cerro Gordo, *Castilla & Tejero 604* (IZTA); Tenango de Tepopula, cerca de Amecameca, *Matuda 18839* (CODAGEM); Teoloyucan, Sierra de Alcaparrosa, *Núñez 43* (IZTA); Tepozotlán, Sierra de Alcaparrosa, *Núñez 2176* (IZTA); Texcoco, 28 km al E de Texcoco, sobre brecha maderera hacia Tlaloc, *García s.n.* (INIF); 10 km al E de Texcoco, al principio de la brecha maderera, *García s.n.* (CHAPA); cerro Tetzcultzingo, 8 km al E de Texcoco, *Pulido 428* (ENCB); 13 km al E de Texcoco, carretera a San Dieguito, *Ricaño 28* (CHAPA); Santa María Tecuanulco, *Ventura 877* (CHAPA, ENCB); Timilpan, Sierra de San Andrés, *Camacho 288, 397* (IZTA); Tlalmanalco, NE de Tlalmanalco, *Medellín 224* (INIF); 3 km al SW de San Rafael Tlalmanalco, *Rodríguez 1033* (ENCB); Tlazala de Fabela, 2 km al SE de Tlazala de Fabela, *Román 289* (ENCB); Valle de Bravo, entre Amanalco de Becerra y Valle de Bravo, *Matuda 28628, 28630* (MEXU); San José Allende, alrededores de San José Allende, *Rojas & Ro-*

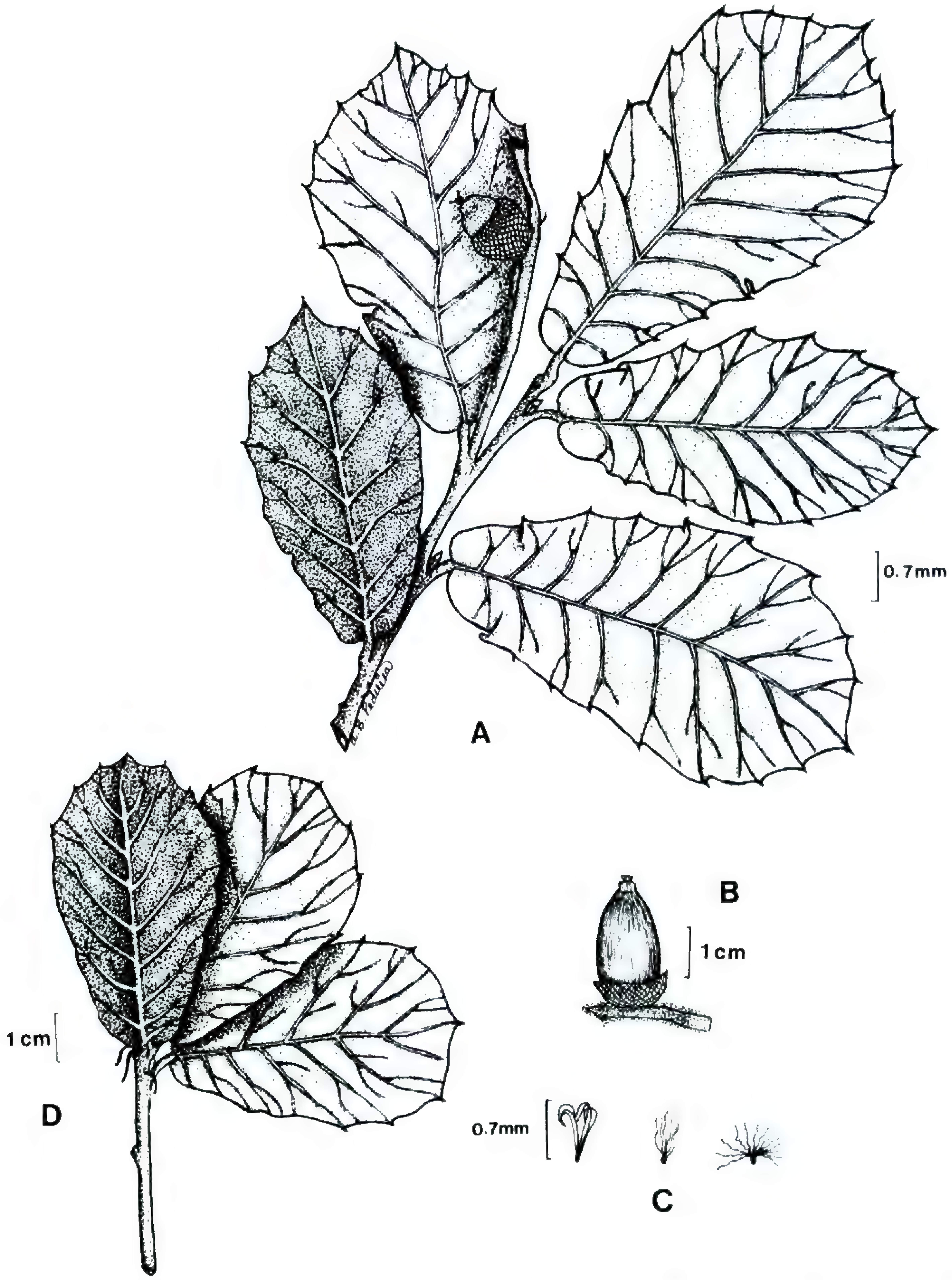

Figura 9. *Quercus rugosa.*—A. Rama. —B. Fruto. —C. Tricomas. —D. Rama. (A–C: *Román 295*; D: *Camacho 160.*)

mero 2057 (IZTA); Villa del Carbón, Predio Piedra Azul, *Ávila s.n.* (INIF); Villa del Carbón, *Matuda 693* (CHAPA); cercanías de Villa del Carbón, *Matuda s.n.* (CHAPA); Villa Victoria, cercanías de Villa Victoria, *Matuda 28620* (CODAGEM).

10. Quercus splendens Née, Anales Ci. Nat. 3: 275. 1801. TIPO: México. Guerrero: cerca de Tixtla, *Née s.n.* (MA).

Árbol de 10–15 m de alto, corteza gris; ramillas de 2 mm diám., rojizas, con la edad cambian a color café claro, con algunos tricomas estrellados

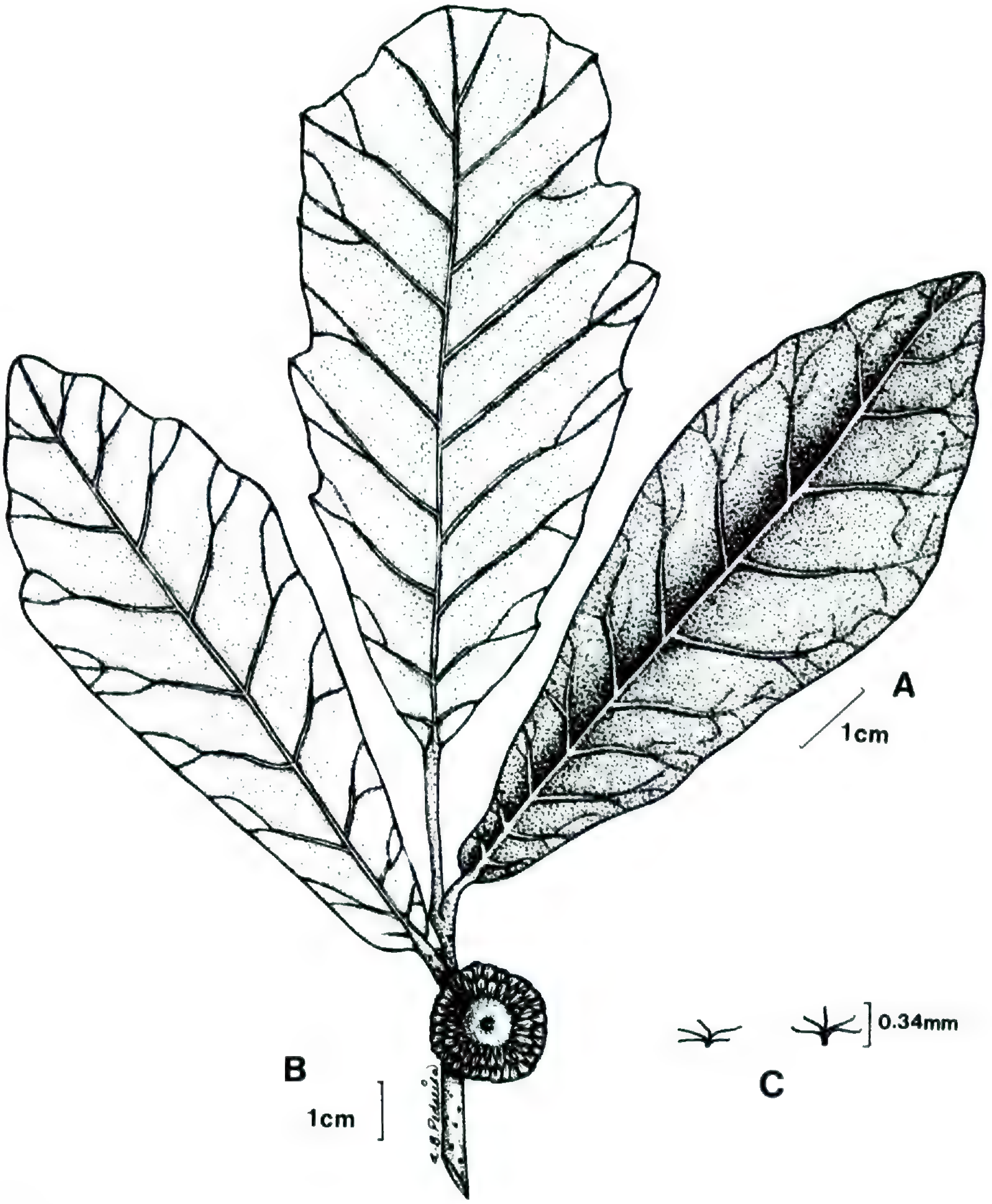

Figura 10. *Quercus splendens.*—A. Rama. —B. Fruto. —C. Tricomas. (*Torres 529.*)

cerca de los pecíolos y yemas, con numerosas lenticelas pálidas, de hasta 1 mm de largo; yemas de 2 o 3 mm de largo, ovoides, de color castaño rojizo; estípulas de 5–8 mm de largo, subuladas, con indumento formado por tricomas largos, persistente en la yema terminal; hojas jóvenes con pubescencia fina, formada de tricomas estrellados dispersos en el haz, envés con tricomas simples y estrellados sobre la nervadura central; hojas maduras decíduas, coriáceas, lanceoladas, elípticas, espatuladas, lámina 7–18 × 2–6 cm, borde ondulado, revoluto, engrosado, cartilaginoso, ápice obtuso o emarginado, base cordada o redondeada; nervaduras de 11 a 14 de cada lado, ascendentes, ligeramente arqueadas, dividiéndose cerca del borde; haz glabro con las nervaduras impresas; envés con pocos tricomas estrellados pequeños y abundantes tricomas simples adpresos a lo largo de la nervadura central, nervaduras prominentes; epidermis glauco-cerosa, papilosa; pecíolos de 5–9 mm de largo, de 1–2 mm diám. en su zona más ancha, rojizos o negros; flores desconocidas; fruto anual, solitario o en grupos de 2 a 3, sésiles; cúpula hemisférica, de 9–16 mm diám., escamas con los ápices triangulares, obtusas, canescentes, engrosadas en la base, sobre todo las basales; bellota oblata, pared interna del pericarpo glabra, de 7–9 mm de largo, de 11–15 mm diám., incluída en su totalidad en la cúpula. Figura 10.

Reconocimiento. Se reconoce por sus hojas verde-azulosas, sin aristas y la pubescencia del envés que tiende a concentrarse en la nervadura central.

Distribución y hábitat. En México en los estados de Durango, Guerrero, Jalisco, Estado de México, Nayarit, Michoacán, Morelos, Sinaloa y Oaxaca. En bosques de *Pinus–Quercus* y bosque tropical caducifolio, en altitudes de 1500–1900 m.

Fenología. Fructifica en julio y agosto.

Nombres populares y usos. Encino.

No se tiene reportado algún uso.

Ejemplares examinados. MÉXICO. **Estado de México**: Amatepec, Amatepec y cercanías, *Matuda 29824* (ENCB); Sultepec, km 18 carretera Sultepec–Salayatla, *Torres 251a* (IZTA); km 12 carretera Sultepec–San Miguel Totolmoloya, *Torres 529* (IZTA); Tejupilco, cerro Nanchititla, *Matuda 31527* (CODAGEM, ENCB); Mesa de Nanchititla, *Matuda 32817* (CODAGEM).

11. Quercus acutifolia Née, Anales Ci. Nat. 3: 267. 1801. TIPO: México. Guerrero: cerca de Tixtla, *Née s.n.* (holotipo, MA!).

Árbol de 12 m de alto, tronco de 30 cm diám.; corteza obscura; ramillas de 1–2.5 mm diám., con costillas, color castaño rojizo, lustrosas, glabras, lenticelas de hasta 0.5 mm, de color claro abundantes; yemas ovoides, con el ápice agudo, de 4–6 mm de largo, escamas ciliadas en sus bordes; estípulas de 5 mm, membranosas, linear-oblanceoladas, decíduas; hojas jóvenes con tricomas simples y estrellados dispersos, más abundantes en la nervadura central; hojas maduras subcoriáceas, rígidas, verdes, envés más pálido, angostamente elípticas, lanceoladas u oblanceoladas, lámina 6.5–14.5 × 2.3–4.2 cm, ápice acuminado o agudo, base obtusa o cuneada, frecuentemente asimétrica, borde cartilaginoso, ligeramente revoluto, con 8 a 10 dientes aristados a cada lado, aristas de hasta 5 mm de largo; nervaduras de 8 a 14 de cada lado, casi rectas, dividiéndose a veces desde la mitad, las nervaduras primarias y secundarias forman aristas; haz glabro, lustroso, nervaduras impresas, la central algo elevada principalmente en la base; envés glabro, lustroso, epidermis lisa, no papilosa, nervaduras elevadas, principalmente la central; pecíolos de 9–22 × 1 mm, glabros, su base más ancha y obscura; flores y frutos desconocidos. Figura 11.

Reconocimiento. *Quercus acutifolia* es muy escasa en el Estado de México; se reconoce por sus hojas dentadas y aristadas y envés casi glabro. *Q. acutifolia* muestra similitud morfológica con *Q. conspersa*, pero esta última se distingue porque el borde de sus hojas es entero y por su envés persistentemente glandular y marcadamente amarillento por la presencia de las glándulas.

Distribución y hábitat. En México en los estados de Jalisco, México y Michoacán. Se le encuentra en bosque mesófilo de montaña, en altitudes menores a los 2200 m.

Fenología. Florece en enero; su fructificación es desconocida.

Nombres populares y usos. Encino sencillo, encino blanco, encino laurelillo, encino tepezcohuite.

La madera se utiliza como leña o para elaborar carbón, postería y pulpa para papel; se recomienda para chapa fina, muebles de alta calidad ebanística, pisos lambrines, cajas para empaque, mangos y cabos para herramienta (De la Paz, 1976).

Ejemplares examinados. MEXICO. **Estado de México**: Valle de Bravo, en parte húmeda, *Boege 1786* (MEXU); Rancho Rincón Grande Tiloxtoc, *Muller 9095* (MEXU).

12. Quercus candicans Née, Anales Ci. Nat. 3: 277. 1801. TIPO. México. Michoacán: Pátzcuaro, *Pringle 3955* (MA).

Árbol de hasta 15 m de alto; tronco hasta de 1 m diám.; ramillas (1.5–)2–3(–3.5) mm diám., con abundante pubescencia amarilla que disminuye con el tiempo, con lenticelas de 1–3 mm de largo, visibles en ramillas con la pubescencia disminuida; yemas ovoides de color castaño, de (2–)3–5(–6) mm de largo, con escamas pilosas; estípulas lineares de 10–15 mm de largo, decíduas; hojas jóvenes algo lustrosas, haz con abundantes tricomas estrellados cortos y tricomas simples dispersos, envés con pubescencia densa blanca, semejante a la de las hojas maduras; hojas maduras coriáceas y gruesas, obovadas, lámina (3.5–)5–19(–23.5) × 3–11(–14) cm, ápice obtuso o agudo, aristado, base subcordada a truncada o estrecha hacia el pecíolo, borde revoluto, cartilaginoso, conspicuamente dentado o dientes mal definidos, hasta con 25 aristas de cada lado distribuidas en las dos terceras partes superiores de la hoja, aristas hasta de 5 mm de largo; nervaduras 8 a 14 cada lado, rectas o ligeramente ascendentes pasando directamente al diente; haz lustroso, de color verde obscuro, con tricomas estrellados y muy dispersos, pero abundantes en la nervadura central cerca del pecíolo, las nervaduras más finas forman un retículo blanco, nervaduras central y primarias impresas o ligeramente elevadas; envés con pubescencia densa blanca que con el tiempo sé amarillenta, formada con tricomas estrellados con muchos rayos, sésiles y pueden presentar un corto estípite; epidermis ampulosa, papilosa, nervaduras elevadas; pecíolo (3–)10–15(–20) × 0.5–1.5 mm, con abundante pubescencia amarilla a rojiza; amentos masculinos laxos, perianto de 2.5–3 mm diám., pilosos en la parte externa y en

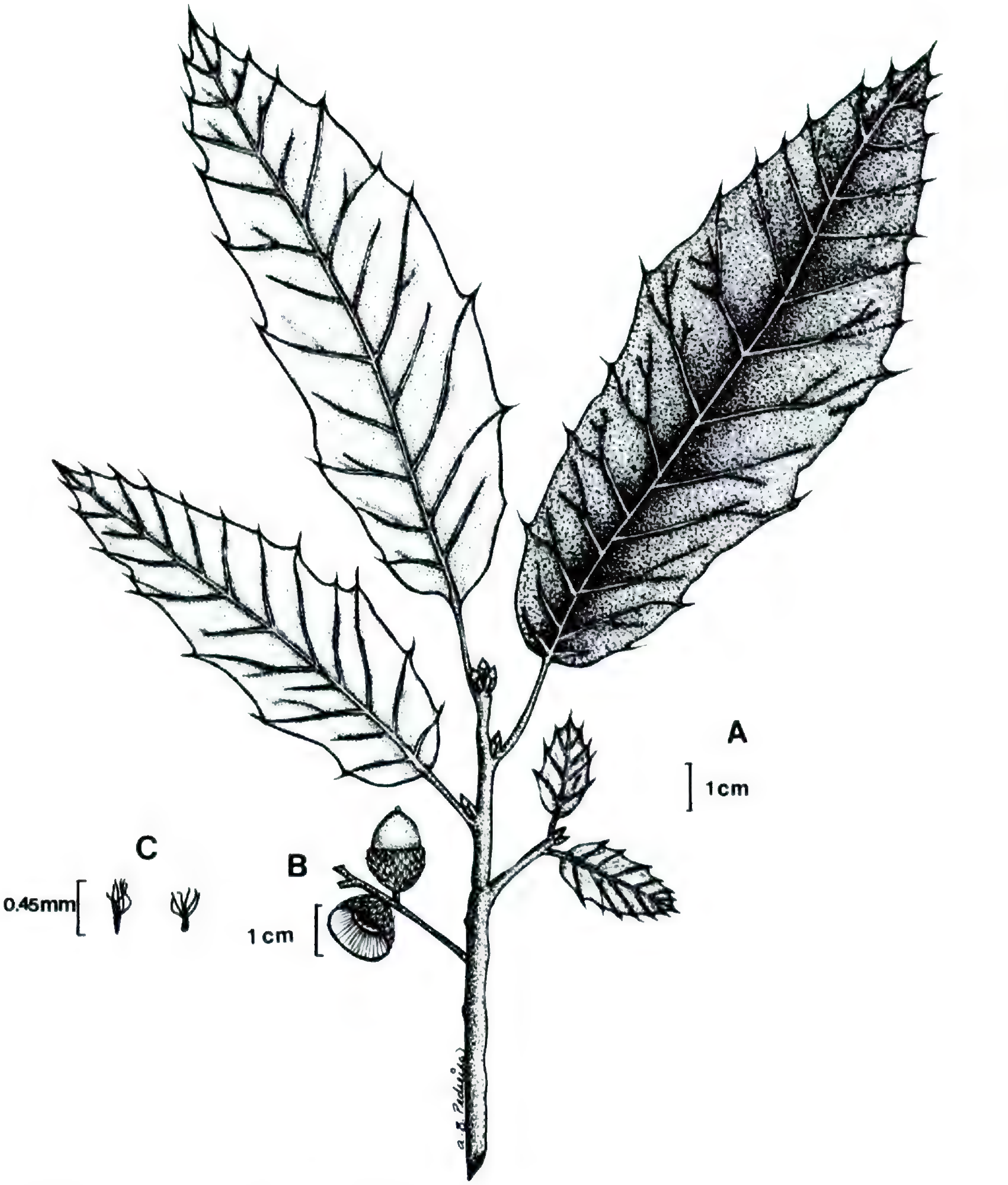

Figura 11. *Quercus acutifolia.*—A. Rama. —B. Fruto. —C. Tricomas. (*Muller 9096.*)

el lugar de inserción de los estambres, anteras exertas de 1.5 mm de largo apendiculadas, filamentos de 2.5 mm de largo; fruto anual o bianual, solitario o en pares sobre pedúnculos de 15 mm de largo, pubescente; cúpula hemisférica de 19–23 mm diám., borde recto, escamas gruesas, con pubescencia corta y muy abundante, ápices redondeados a agudos, glabros; bellota de 20 mm de largo, de 17 mm diám., anchamente ovoide, incluida un tercio de su largo en la cúpula. Figura 12.

Reconocimiento. Se reconoce por sus hojas con dientes aristados, haz verde lustroso y envés con pubescencia blanca.

Distribución y hábitat. En México en los estados de Chiapas, Chihuahua, Durango, Guanajuato, Hidalgo Jalisco, Estado de México, Nayarit, Oaxaca y Sinaloa, también en Guatemala. Se le encuentra de manera escasa o abundante en bosques de *Quercus*, *Quercus–Pinus* y bosque mesófilo de montaña, y se asocia con *Clethra*, en altitudes de 2000–2600 m.

Fenología. Florece en mayo y fructifica en noviembre.

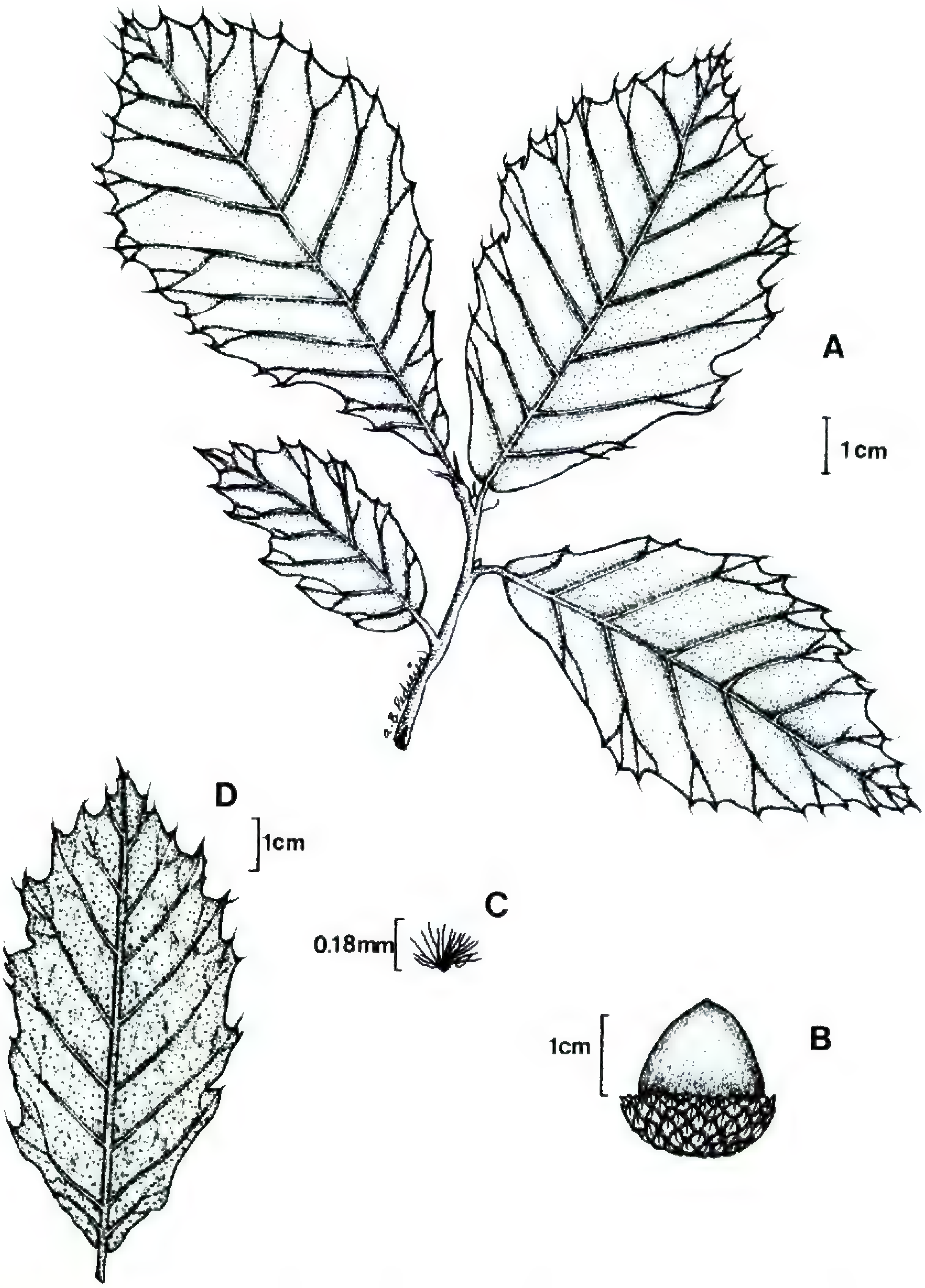

Figura 12. *Quercus candicans*.—A. Rama. —B. Fruto. —C. Tricoma. —D. Hoja. (*Rodríguez s.n.*)

Nombres populares y usos. Encino de asta, encino cenizo, encino papatla, encino blanco, ahuamextli.

Su corteza se usa para dolor de muelas; su efecto dura hasta 15 días. De la Paz (1976) propone que se utilice para muebles y gabinetes de alta calidad ebanística, chapa fina, pisos para residencias, marcos para puertas y ventanas, cajas de empaque, cofres, mangos y cabos de herramientas e implementos agrícolas.

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, ladera S del cerro Hoyo de Lobo, *Rojas & Romero 2059-A* (IZTA); Coatepec de Harinas, 4 km al E de Coatepec de Harinas, *Martínez 2845* (MEXU); 3 km al NE de Coatepec de Harinas sobre el camino a Agua Amarga, *Rzedowski 30356* (ENCB); Huixquilucan, alrededores de Dos Ríos, *Román 317* (ENCB); 1 km al NW de Santiago Yancuitlalpan, *Rzedowski 33489* (ENCB, MEXU); Jilotepec, Cerro de Jilotepec, *Matuda 29054* (CODAGEM, ENCB, MEXU); Santa Ana Jilotzingo, Sierra del Monte Alto, 3 km al NW de Santa Ana Jilotzingo, *Rzedowski 22412* (ENCB, MEXU); Ixtapan de la Sal, km 106 de la carretera a Ixtapan de la Sal, *Martínez 2847* (MEXU); Malinalco, en ladera húmeda, *Matuda 28814* (CODAGEM,

MEXU); Ocuilan de Arteaga, km 18 de la terracería Ocuilan–Cuernavaca, *Cortés 25* (IZTA); 1 km al S de Ocuilan de Arteaga, *Muller 9218* (MEXU); Sultepec, km 16 carretera Sultepec–San Miguel Totolmoloya, *Torres 302* (IZTA); Temascaltepec de González, Comunal de Tequisquiapan, *Huerta & Ramos T-14* (ENCB, MEXU); El Guajero, rumbo a Real de Arriba, *Rojas & Romero 2370* (IZTA); km 57 carretera Toluca–Temascaltepec, *Rojas & Romero 2426* (IZTA); km 51 Toluca–Temascaltepec, *Rojas & Romero 3210* (IZTA); Tenancingo, Tenancingo, *Martínez 65* (MEXU); Tenango de Arista, Rancho Yeca, *Ávila s.n.* (ENCB, IZTA); Villa del Carbón, El Plan, *González s.n.* (IZTA); San Jerónimo, *Matuda 28774* (MEXU); Cerro Bufa, *Matuda 29753* (MEXU); Villa Guerrero, 5 km al N de Villa Guerrero, *Roe & Roe s.n.* (ENCB); Villa Nicolás Romero, km 8 carretera Villa Nicolás Romero–Tlazala, límite municipal de Villa Nicolás Romero, *Quintero 33* (IZTA); Barrio IV, *Rojas & Romero 3191* (IZTA); Cahuacán, *Rojas & Romero 3191 A* (IZTA); 3 km al NW de Cahuacán, *Rzedowski 32626* (ENCB).

13. Quercus castanea Née, Anales Ci. Nat. 3: 276. 1801. TIPO: México. Hidalgo: *Née s.n.* (MA).

Quercus axillaris Fourn. ex Trel., Mem. Natl. Acad. Sci. 20: 176, pl. 352. 1924. TIPO: México. San Nicolás, Valle de México, *Bourgeau 1138* (B).
Quercus pulchella Humb. & Bonpl., Pl. Aequinoct. 2: (38)44, pl. 88. 1809. TIPO: México. Guanajuato: Santa Rosa, *Bonpland s.n.* (P).

Árbol de 5–15 m de alto, tronco de 40–80 cm diám.; ramillas de (0.5–)1–2 mm diám., de color café claro a obscuro, pubescentes, a veces glabras con varias costillas, lenticelas pálidas de 0.5–1 mm de largo; yemas de (1–)2–3.5(–7) mm de largo, ovoides o agudas, de color café, con escamas ovadas, ciliadas en los márgenes y dorso superior, coriáceas; estípulas de 5–6 mm de largo, lanceoladas, de color claro, membranosas, con tricomas largos principalmente en los márgenes, caedizas muy pronto; hojas jóvenes muy parecidas a las maduras, haz verde con pubescencia principalmente en la base y nervaduras, envés densamente pubescente; hojas maduras gruesas, elípticas, elíptico-oblongas, oblanceoladas o lanceoladas, láminas (1.8–)3–9(–11.6) × 1–4(–5.5) cm, ápice agudo u obtuso, aristado, base redondeada a cordada, borde plano o ligeramente revoluto, entero o dentado, con 1–7 aristas de hasta 2 mm de largo, en cada lado del tercio o mitad superior; nervaduras primarias de (3–)5–12 en cada lado, ascendentes, se ramifican y reticulan cerca del borde, generalmente se continúan en una arista; haz verde claro a obscuro, lustroso, finamente rugoso por las nervaduras, glabro excepto cerca del pecíolo, nervadura central elevada principalmente en la base, nervaduras primarias y secundarias impresas, las menores forman un retículo pálido; envés muy pubescente, la abundancia de tricomas disminuye con la edad, pubescencia grisácea, formada de tricomas estrellado-estipitados, sus rayos rugosos y enredados, epidermis con ámpulas prominentes, nervaduras conspicuamente elevadas, pálidas; pecíolos de (2.5–)4–10(–15) × 0.5–1.5 mm, se ensanchan en la base, pubescente o glabros; amentos masculinos de 6 cm de largo, pedúnculos pubescentes, perianto de 1.5–2 mm diám., bordes ciliados, anteras de 1.5 mm de largo, filamentos de 1 mm de largo; amentos femeninos con 1 o 2 flores, pedúnculos de 3–5 mm de largo, con pubescencia muy corta formada de tricomas estrellados; fruto anual, 1 o 2 sésiles o sobre un pedúnculo de 1–7 mm de largo; cúpula hemisférica de 9–14 mm diám., con escamas algo engrosadas en la base, ápice obtuso y papiráceo, pubescentes a casi glabras, de color café rojizo; bellota anchamente ovoide, pared interna del pericarpo lanosa, de 5–15 mm de largo y de 8–11 mm diám., incluida en la cúpula de un tercio a un medio de su largo. Figura 13.

Reconocimiento. Esta especie se reconoce por sus hojas aristadas y envés con las nervaduras conspicuamente elevadas y reticuladas.

Distribución y hábitat. En México en los estados de Colima, Distrito Federal, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, Estado de México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, San Luis Potosí, Sonora, Sinaloa y Veracruz, también en Guatemala. Se encuentra en bosques de *Pinus*, *Quercus* y *Pinus–Quercus*, pastizal con matorral xerófilo y bosque mesófilo de montaña; es frecuente encontrarla en encinares perturbados. Se le ha visto asociada con *Quercus obtusata*, *Q. glaucoides*, *Q. conspersa*, *Clethra*, *Arbutus* y *Pinus michoacana*, en altitudes de 1900–3500 m.

Fenología. Florece en junio–julio y fructifica de agosto a diciembre.

Nombres populares y usos. Encino, encino blanco, encino negro, encino amarillo, encino rojo, palo colorado, encino pipitillo, roble, encino prieto, tepozcohuite chino, encino chaparro, encino colorado y aguacatillo.

De la Paz (1982) recomienda su madera para pisos de residencias, vehículos (de motor y no motorizados), tarimas para carga y descarga, mangos y cabos de herramienta, implementos agrícolas, y diversos tipos de recipientes y armazones de construcción.

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, Cerro Hondingá, *Torres 1442* (IZTA); Almoloya del Río, Cerro de San Andrés, *Rodríguez 147* (ENCB); Amecameca, 1 km al NW de San Antonio Zoyatzingo, *Reyes 211* (ENCB, MEXU); Atizapán, vertiente SE del cerro Chiluca, 6 km al SW de Ciudad Adolfo López

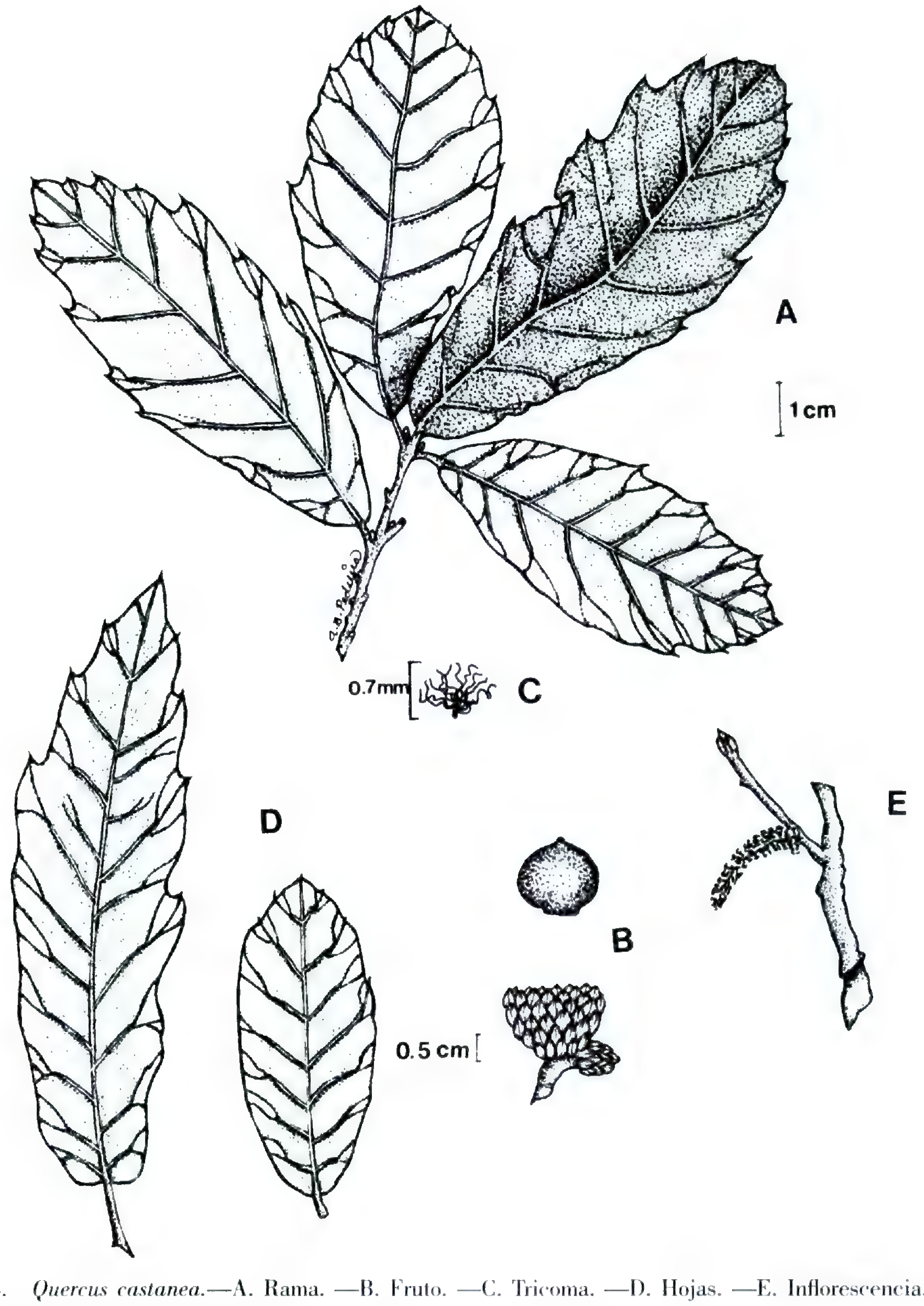

Figura 13. *Quercus castanea*.—A. Rama. —B. Fruto. —C. Tricoma. —D. Hojas. —E. Inflorescencia. (A–E: *Rodríguez s.n.*)

Mateos, *Patiño 335* (ENCB); vertiente SE del cerro Chiluca, *Polaco 214, 335* (ENCB); Cerro de Tigre, al NW de Ciudad Adolfo López Mateos, *Rzedowski 32036* (ENCB, MEXU); parte alta del cerro Chiluca, cerca de Ciudad Adolfo López Mateos, *Rzedowski 32586* (ENCB, MEXU); El Oro de Hidalgo, entre el Oro y Villa Victoria, *Matuda 28644* (CODAGEM, MEXU); cercanías del Oro, *Matuda 28646* (ENCB); Huixquilucan, entre San Bartolo y Toluca, *Espinosa 495* (ENCB); 2 km al N de San Bartolito, *García 189* (ENCB); Magdalena, *Rzedowski 21954* (ENCB); Ixtapaluca, La Cañada, *Vela s.n.* (CHAPA); Jilotepec, Cañada Ojo de Agua, *Romero & Rojas 3065* (IZTA); Santa Ana Jilotzingo, Sierra del Monte Alto, 3 km al NE de Santa Ana Jilotzingo, *Rzedowski 22414* (ENCB); Malinalco, Malinalco, *Matuda 28776* (ENCB); Naucalpan de Juárez, Naucalpan de Juárez, *COTECOCA 15072* (ENCB); alrededores de San Francisco Chimalpa, *Rzedowski 20117* (ENCB, MEXU); 8 km al W de San Bartolo, *Rzedowski 32243* (ENCB, MEXU); Ocuilan de Arteaga, El Ahuehuete, *Rzedowski 26922* (ENCB); Otzoloapan, Cerro de Pinal, *Matuda s.n.* (CODAGEM, MEXU); Polotitlán, km 147 carretera a Toluca, *Rojas & Romero 3099* (IZTA); San Felipe del Progreso, entre el Oro y Villa Victoria, *Matuda 28644* (ENCB); Nuevo Santo Tomás de los Plátanos, cerca de Nuevo Santo Tomás de los Plátanos, *Matuda 29385* (ENCB); Sultepec, Real de Abajo, *Matuda 29300* (ENCB, MEXU); 2 km al NE de Sultepec, *Rodríguez 166* (ENCB); km 18 carretera Sultepec–San Miguel Totolmoloya, *Torres*

317 (IZTA); Tejupilco, Nanchititla, *Rodríguez 199* (ENCB, MEXU); Temascaltepec de González, Tenería, *Guízar 499* (MEXU); San Lucas del Pulque, *Hinton 6738* (MEXU); Real de Arriba, *Huerta RA-1* (ENCB); Temascaltepec de González, *Matuda 26612* (ENCB); La Labor, *Matuda 2763* (ENCB, MEXU); Estancia Vieja, 10 km al S de Temascaltepec de González, *Moreno 147* (ENCB); km 4 Valle de Bravo–Temascaltepec, dirección a San Lucas del Pulque, *Orozco & Rojas 520 E* (IZTA); Barrio la Mesa, pasando Tequesquipan, *Orozco & Rojas 610 A* (IZTA); km 9 Valle de Bravo–Temascaltepec, dirección a la Albarrada, *Orozco 284 E* (IZTA); 5 km al SW de Temascaltepec de González, *Rzedowski 20830* (ENCB); Tenancingo, Tenancingo, *Martínez 698* (ENCB); Tenancingo, *Muller 697* (MEXU); 10 km al N de Tenancingo, *Muller 9194* (ENCB); Comunal Real de Arriba, *Ramos & Rocha s.n.* (MEXU); Tenango, entre Tenango y Chulem, *Martínez s.n.* (ENCB); Tepotzotlán, 2 km al N de Magú, *Cruz 493, 496* (ENCB, MEXU); Sierra de Alcaparrosa, *Núñez 1710* (IZTA); Cercanías de la Presa Concepción, *Rzedowski 22908* (ENCB); parte baja de la Sierra de Alcaparrosa, 2 km al NNW de Tepotzotlán, *Rzedowski 29908* (ENCB); Tlatlaya, Tlatlaya y cercanías, *Matuda 29829* (CODAGEM, ENCB, MEXU); Valle de Bravo, Valle de Bravo, *Martínez 2612* (ENCB); Godines Tehuastepec, *Rodríguez 204* (ENCB); Villa del Carbón, 5 km al W de Progreso Industrial, *Rzedowski 2600, 35261* (ENCB, MEXU); Villa Guerrero, Villa Guerrero, *COTECOCA 15077* (ENCB); Villa Nicolás Romero, 3 km al E de Cahuacán, *Espinosa 621* (ENCB); Cahuacán, *Germán & Trejo 43* (MEXU); km 32 carretera Tlalnepantla–Villa del Carbón, *Rojas & Romero 2019* (IZTA); 1 km al S de Cahuacán, *Rzedowski 16815* (ENCB); Zacualpan, km 3–4 carretera Zacualpan–Mamatla, *Fragoso 340* (IZTA).

14. Quercus conspersa Bentham, Pl. Hartw. 91. 1842. TIPO: Guatemala. Las Casillas, *Hartweg 617* (isotipo, NY!).

Árbol de 9 m de alto, tronco de 50 cm diám., corteza obscura; ramillas de 2–3 mm diám., glabras, de color castaño rojizo; lenticelas numerosas, blancas, protuberantes, de hasta 0.5 mm de largo; yemas de 2–3 mm de largo, ovoides, ápice agudo, con escamas ciliadas en sus bordes, de color castaño-rojizo; estípulas de 7–8 mm de largo, lineares, pilosas; persistentes en las hojas jóvenes; hojas jóvenes rojizas, haz con tricomas simples y estrellados, escasos y dispersos, envés con abundantes tricomas glandulares de color ámbar y estrellados con un largo estípite y rayos enredados entre sí, abundantes en las axilas de las nervaduras primarias; hojas maduras gruesas, coriáceas, decíduas, elíptico-ovadas, lanceoladas u oblanceoladas, lámina (8–)11–17(–22) × (2–)3–6.5 cm, ápice acuminado o agudo aristado, base obtusa, subcordada o atenuada, a veces asimétrica, borde grueso, cartilaginoso, revoluto, entero; nervaduras primarias de 7 a 10 en cada lado, ascendentes, en hojas elíptico-ovadas son casi paralelas, ramificándose, a veces, desde la base de la nervadura hasta cerca del borde; haz lustroso, de color olivo, glabro, excepto en la nervadura central en la que se observan abundantes tricomas glandulares obscuros y tricomas estrellados pequeños en la base de la hoja, nervaduras impresas, envés también lustroso, amarillento por la presencia de tricomas glandulares color ámbar, con mechones de tricomas estrellados con estípite largo y rayos enredados entre sí, concentrados en las axilas de las nervaduras primarias, epidermis papilosa, nervaduras prominentes; pecíolos de 8–15 mm de largo, engrosados en su base, de color rojizo a negro, en un principio pubescentes, luego glabros-rugosos; flores desconocidas; fruto bianual, solitario, sobre un pedúnculo grueso, de 4–6 mm de largo; cúpula poco profunda, de 14 mm diám., borde enrollado; escamas con pubescencia blanca, adpresas, no engrosadas en la base, ápices deltoides u obtusos; bellota comprimida, pared interna del pericarpo lanosa, de 5 mm de largo, de 10 mm diám., la mitad de su longitud incluida en la cúpula. Figura 14.

Reconocimiento. *Quercus conspersa* se reconoce por sus hojas de borde entero, haz lustroso de color verde-olivo y envés amarillento por la presencia de tricomas glandulares. Esta especie se confunde con *Q. acutifolia* (ver *Q. acutifolia*).

Distribución y hábitat. En México en los estados de Chiapas, Guerrero, Jalisco, Estado de México, Michoacán, Oaxaca y Veracruz, también en América Central. Se le encuentra en bosque de *Quercus–Pinus*, y se le encuentra asociado a *Pinus oocarpa*, en altitudes menores de 2000 m.

Fenología. Fructifica de diciembre a febrero.

Nombres populares y usos. Encino, roble amarillo, encino rojo, encino colorado, encino pipitillo, tepozcohuite, encino cáscara, encino blanco.

Su madera es utilizada para la elaboración de chapa y pulpa para papel (González, 1986).

Ejemplares examinados. MÉXICO. **Estado de México**: Temascaltepec de González, Pungarancho, *Hinton 7570* (MEXU); 0.5 km al SE de Albarrada, 7 km al W de Temascaltepec de González, *Muller 9104* (MEXU); km 15 desviación San Pedro Tenayac, *Orozco 144* (IZTA).

15. Quercus crassifolia Humboldt & Bonpland, Pl. Aequinoct., 2: 49, pl. 91. 1809. TIPO: México. Guerrero: Chilpancingo, *Bonpland s.n.* (B, P).

Arbolillo de 2–3 m de alto o árbol de hasta 15 m de alto, tronco hasta de 1 m diám., ramillas de 2–5 mm diám., con abundantes tricomas estrellados estipitados cubriendo totalmente la superficie, pubescencia amarilla a café que se obscurece y cae con el tiempo; lenticelas numerosas de hasta 3 mm,

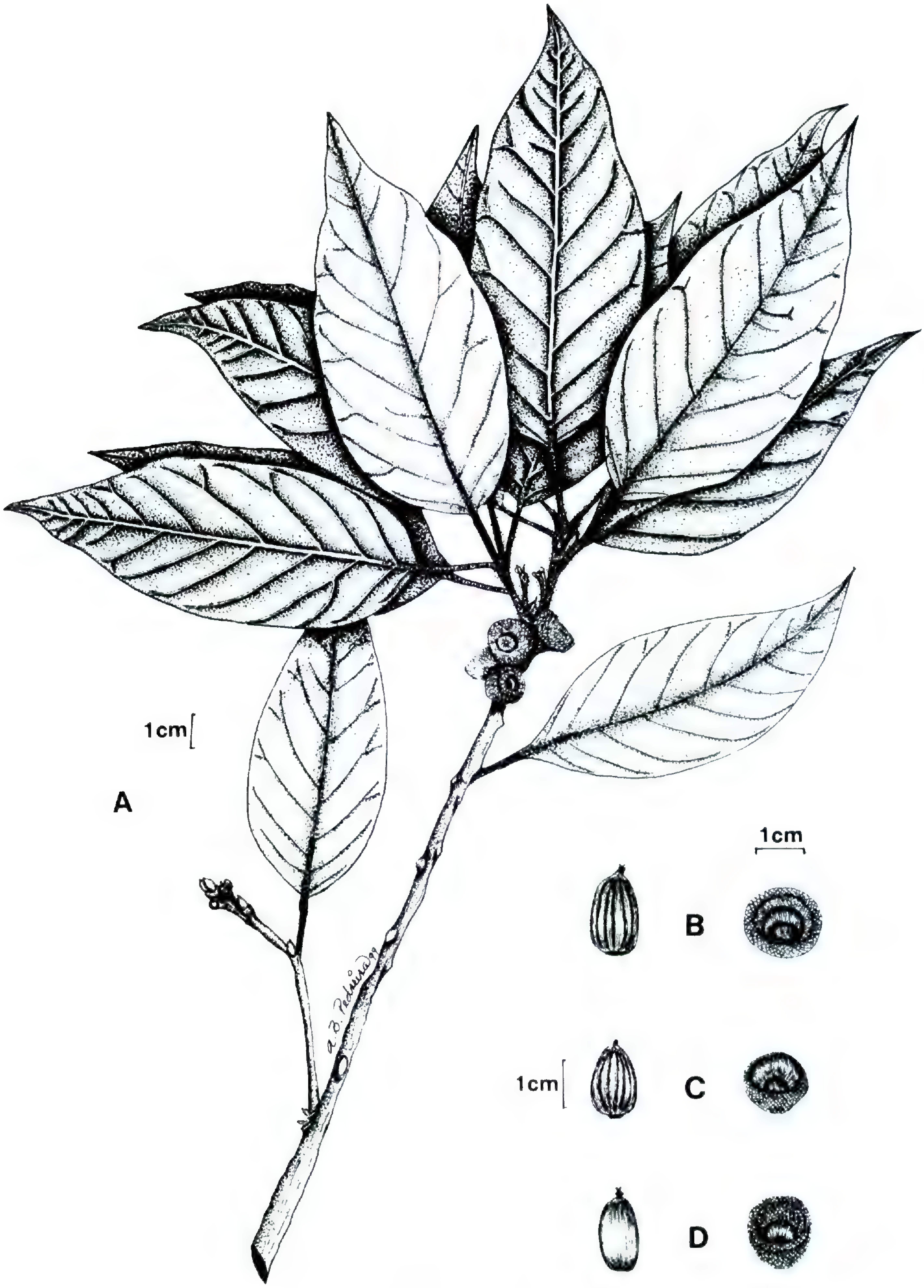

Figura 14. *Quercus conspersa.*—A. Rama. —B–D. Frutos. (*Hinton 7570.*)

claras, visibles sólo en las ramas que han perdido la pubescencia; yemas de 3–7 mm, ovoides, pilosas; estípulas de 8–12 mm de largo, oblanceoladas, escariosas, sedoso pubescentes, con el tiempo glabras, persistentes en las yemas, a veces también en las hojas maduras; hojas jóvenes lanoso-tomentosas, haz rojizo y envés café, con aristas de hasta 3 mm de largo, indumento formado por tricomas estrellados estipitados y glandulares rojizos sobre la epidermis obscura; hojas maduras por lo general obovadas, oblongo-obovadas, elípticas, coriáceas, lámina (4.5–)7–17(–20) × 3.5–10(–11.5) cm, ápice

agudo, acuminado u obtuso, aristado, base cordada o redondeada, borde ondulado o dentado, revoluto, cartilaginoso, de 3 a 8 dientes en cada lado, ubicados casi desde la base de la hoja, 1 a 10 aristas, dientes y aristas con frecuencia asimétricos; nervaduras 6 a 12 a cada lado, ascendentes, ramificándose cerca del borde, pasan directamente a los dientes y forman las aristas, con frecuencia hacen lo mismo las ramificaciones; haz lustroso, glabro, excepto la nervadura central que posee abundantes tricomas estrellados, sobre todo cerca del pecíolo, nervaduras impresas; envés amarillo anaranjado o café, lanoso-tomentoso, indumento formado por tricomas estrellados con un largo estípite, sus ramas muy largas y entrelazadas, cubriendo la epidermis ampulosa y papilosa, nervaduras elevadas; pecíolo con pubescencia densa formada por tricomas estrellados más cortos que los del envés, ensanchado en su base, de 6–15(–17) × (1–)2–3 mm; amentos masculinos de 8–9 mm de largo, raquis pubescente, perianto amplio, de 2–2.5 mm diám., anteras curvadas de 2 mm de largo, amarillentas-cafés, apendiculadas; fruto anual o bianual, solitario o en pares, sésiles o en pedúnculos de 3–5 mm de largo; cúpula hemisférica, de 11–13 mm diám., con las escamas delgadas adpresas, pubescentes, principalmente en sus ápices, éstos redondeados; bellota ovoide, pared interna del pericarpo lanosa, de 10–17 mm de largo, de 8–11 mm diám., incluida en la cúpula ⅓ de su largo. Figura 15.

Reconocimiento. *Quercus crassifolia* se reconoce por sus hojas aristadas con el envés lanoso amarillo, anaranjado o café y ramillas de 1–5 mm diám. Esta especie muestra similitud con *Q. hintonii*; ésta última se distingue porque el envés de sus hojas posee epidermis lisa y las ramas de los tricomas estrellados son más largas. En ocasiones también puede confundirse con *Q. dysophylla*, pero ésta última posee hojas de forma ovada, lanceolada o elíptica, por lo general de borde entero; mientras que *Q. crassifolia* casi siempre las presenta obovadas o dentadas. Además los pecíolos son más cortos en *Q. dysophylla*.

Distribución y hábitat. En México en los estados de Chiapas, Guerrero, Hidalgo, Jalisco, Estado de México, Michoacán, Oaxaca, Puebla, Querétaro, San Luis Potosí, Tlaxcala y Veracruz, también en Guatemala. Se le encuentra en bosques de *Quercus*, y *Quercus–Pinus*, se asocia con *Pinus leiophylla*, *Q. laurina* y *Q. crassipes*, y se le ha encontrado en zonas de regeneración después de incendios, en altitudes de 2500–2800 m.

Fenología. Florece en abril y fructifica en octubre.

Nombres populares y usos. Encino chicharrón, encino colorado, encino prieto, encino roble, encino hojarasco, encino huaje, chi-ka-chi, hoja ancha.

La madera de esta especie se utiliza para la manufactura de implementos agrícolas, para horcones de casas, mangos de herramientas y leña; el carbón obtenido de esta especie resulta durable y de buen peso (Camacho, 1985); los retoños son comidos una vez cocidos, molidos y mezclados con maíz; junto con carrizo de monte, sauco, toronjil y zarza se emplea para hacer un agua caliente para mujeres después del parto; la corteza se usa para aliviar dolores de encías, para curtir pieles y en la preparación de bebidas de *Agave* (Pennington, 1969).

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, *Martínez s.n.* (ENCB); Aculco de Espinosa, *Martínez 28739* (MEXU); Axapusco, Cerro del Tipayo, *Ventura 557* (ENCB); Coatepec de Harinas, sobre el camino de Agua Amarga, *Rzedowski 30351* (ENCB); Capulhuac, *Rodríguez s.n.* (ENCB); El Oro de Hidalgo, Bassoco, *Rojas & Romero 3326, 3328* (IZTA); Jilotepec, Denhxi, *Martínez 63* (IZTA); Las Peñas, *Rojas & Romero 2064, 3075, 3081, 3077* (IZTA); Jilotepec, Jilotepec, *Martínez 26704* (ENCB); Peña Descani, *Martínez s.n.* (MEXU); Jilotepec, *Matuda 26673* (ENCB); Cerro de Jilotepec, *Matuda 29058* (CODAGEM); Santa Ana Jilotzingo, Sierra de Monte Alto, al NE de Santa Ana Jilotzingo, *Rzedowski 22411* (ENCB); Temascaltepec de González, San Francisco Oxtotilpan, región Matlatzinca, *Fragoso R. 253* (IZTA); Timilpan, Sierra de San Andrés, *Camacho 153, 233, 293, 419* (IZTA); 4 km al W de la cabecera municipal, *Gómez & Mendoza 4* (IZTA); Tlazala de Fabela, alrededores de Tlazala de Fabela, *Román 275* (MEXU); 2 km al SE de Tlazala de Fabela, *Román 290* (ENCB); Villa del Carbón, Cerro de la Cabra, *Bringas s.n.* (ENCB); 1 km al SE de Villa del Carbón, *Cruz 169* (ENCB); Cerro La Bufa, *Martínez s.n.* (MEXU); cercanías de Villa del Carbón, *Matuda 28767* (ENCB); San Jerónimo, *Matuda 29017* (CODAGEM); San Jerónimo, *Matuda 29160* (ENCB); km 15 Jiquipilco–Villa del Carbón, *Rojas & Romero 3175* (IZTA); El Plan, *Rodríguez s.n.* (IZTA); Villa Nicolás Romero, 5 km al SW de Cahuacán, *González 876* (ENCB); 5 km al NW de Cahuacán, sobre el camino a Villa del Carbón, *Rzedowski 18310* (ENCB, MEXU); 2 km al NW de Cahuacán, *Rzedowski 33755*.

16. Quercus crassipes Humboldt & Bonpland, Pl. Aequinoct. 2: 37. Pl. 83. 1809. TIPO: México. Guanajuato: Santa Rosa, *Bonpland s.n.* (isotipo, B!).

Árbol de 4–17 m de alto o más, con el tronco de 0.40–1 m diám.; corteza de placas alargadas o de color obscuro; ramillas de (5–)1–2 mm diám., con pubescencia densa amarilla, formada por tricomas estrellados con estípite muy pequeño; lenticelas hasta de 1 mm de largo, desde pálidas hasta del mismo color de las ramas; yemas de 1.5–4.5 mm de largo, ovoides, de color café-rojizo, escamas coriáceas, bordes ciliados; estípulas de 7–8 mm de

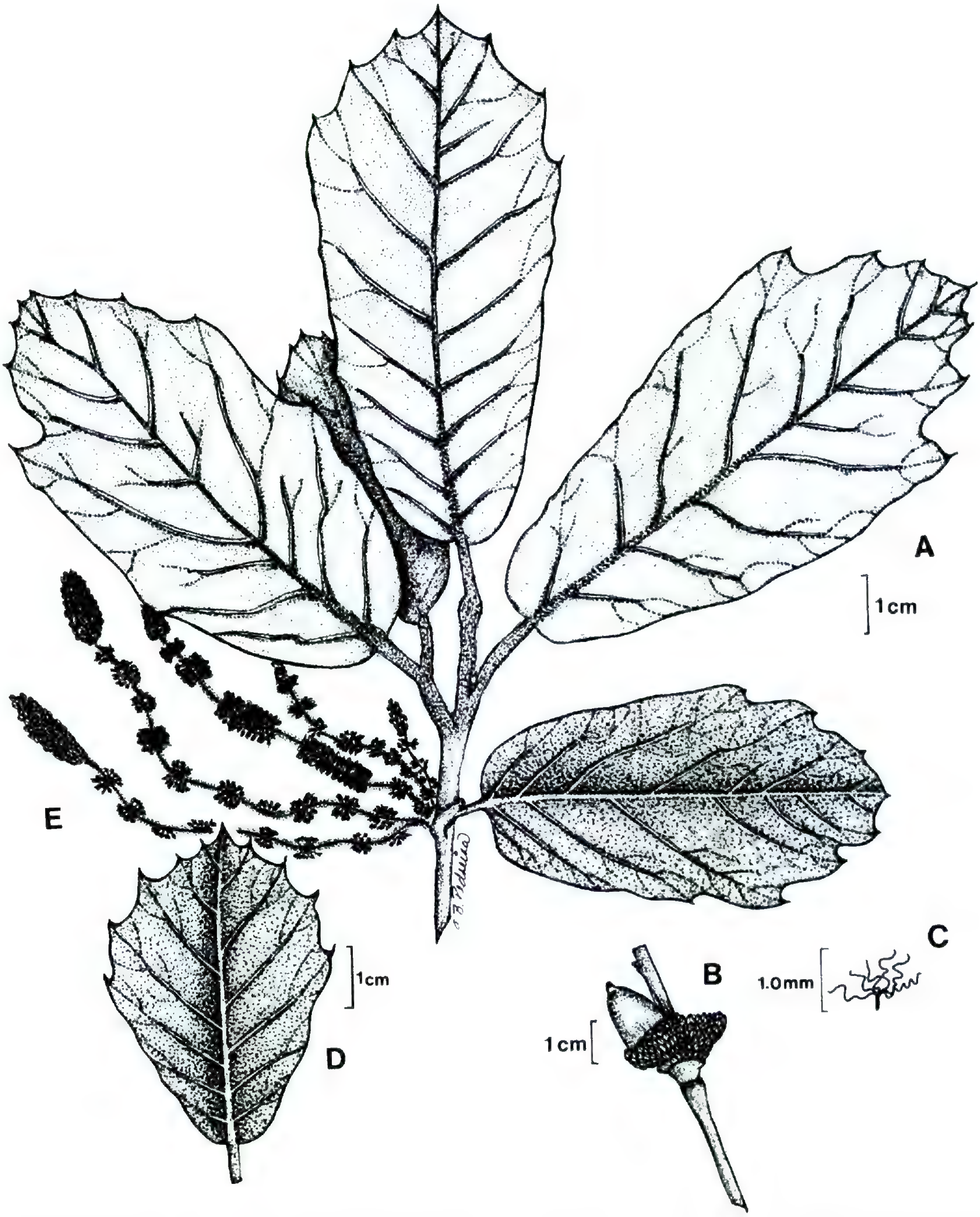

Figura 15. *Quercus crassifolia.*—A. Rama. —B. Fruto. —C. Tricoma. —D. Hoja. —E. Inflorescencia. (A: *Romero 3081*; B–D: *Camacho 153*.)

largo, linear-lanceoladas, membranosas pubescentes en el dorso, decíduas; hojas jóvenes con abundante pubescencia amarilla en haz y envés, principalmente en la nervadura central; hojas maduras coriáceas, angostamente elípticas, lanceoladas u oblanceoladas, lámina 2–9(–10.8) × (0.6–)1–3(–4) cm, ápice mucronado o con arista de 3 mm de largo, base redondeada o subcordada, borde entero, revoluto, engrosado; nervaduras de 10 a 19 en cada lado, rectas o algo curvadas, formando ángulos casi rectos, bifurcados cerca del margen; haz algo lustroso, color verde o grisáceo, glabro o con pequeños tricomas estrellados dispersos, muy abundantes en la base de la hoja, nervadura central elevada, las primeras impresas, las más finas forman un retículo pálido sobre un fondo verde; envés con pubescen-

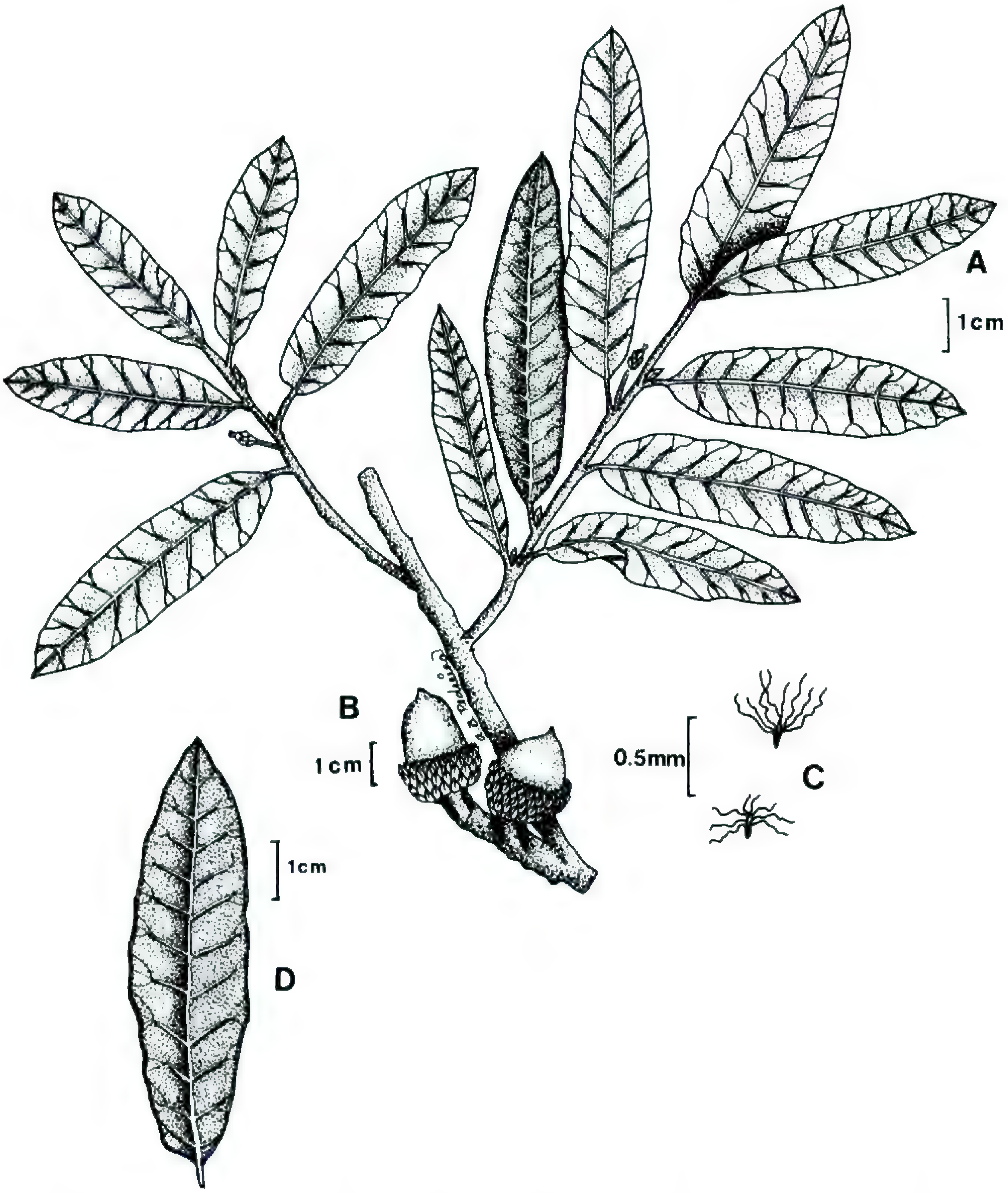

Figura 16. *Quercus crassipes.*—A. Rama. —B. Fruto. —C. Tricomas. —D. Hoja. (A–C: *Romero 2055*; D: *Acosta 26.*)

cia densa, grisáceo, tricomas estrellados estipitados, con 5 a 6 rayos extendidos, epidermis ampulosa; nervaduras ligeramente elevadas; pecíolos amarillentos o rojizos, pubescentes o casi glabros, (1–)2–7(–10) mm de largo, de 0.5–1 mm diám.; amentos masculinos de 4–5.5 cm de largo; flores con el perianto escarioso de 4 × 3 mm, café-rojizo, pubescentes; estambres 5, de 3 mm de largo, anteras apiculadas; flores femeninas de 1 o 2 sobre pedúnculos de 5 mm de largo o menos, de 2–2.5 mm diám.; fruto bianual, solitario o por pares en pedúnculos de 2–8 mm de largo; cúpula hemisférica, de 11–17 mm diám., márgenes a veces involutos, las escamas engrosadas en la base, pubescentes, a veces glabrescentes; bellota ovoide, pared interna del pericarpo lanosa, de 12–17(–30) mm de largo, de 8–15 mm diám., cerca de la tercera parte de su largo incluida en la cúpula. Figura 16.

Reconocimiento. Quercus crassipes se reconoce por sus hojas con el ápice aristado y las nervaduras que forman ángulos casi rectos; muestra similitud con *Q. mexicana*. Ésta se diferencia porque el envés de la hoja posee tricomas estrellados con sus

ramas enredadas entre sí, de manera que a simple vista se observan como puntuaciones.

Distribución y hábitat. En México en los estados de Jalisco, Guanajuato, Querétaro, Hidalgo, Colima, Michoacán, Estado de México, Distrito Federal, Morelos, Tlaxcala y Puebla. Se le encuentra en bosques de *Quercus*, *Pinus–Quercus* y *Quercus–Cupressus*, bosque mesófilo de montaña, matorral xerófilo, en sitios de transición de pastizal a bosque mixto; se asocia con *Pinus pseudostrobus*, *P. leiophylla*, *P. montezumae* y *P. hartwegii*, *Quercus laurina*, *Q. crassifolia*, *Q. obtusata* y *Q. castanea*, en altitudes de 1900–3500 m.

Fenología. Florece en mayo y fructifica de septiembre a enero.

Nombres populares y usos. Encino, encino colorado, encino chilillo, encino oreja de ratón y encino laurel.

De la Paz (1982) recomienda su madera para pisos de residencias, auditorios, museos, almacenes, pistas de baile (en forma de parquet y adoquín), para chapa fina, muebles y gabinetes de alta calidad ebanística, lambrín, decoración de estudios y corredores, cocinas integrales, baúles, canastos, macetas, cofres y diversos artículos decorativos, mangos para herramientas, lomos y mangos de cepillos, brochas y de utensilios de cocina, pasamanos, huellas (escalones) y descansos de escaleras, hormas para zapatos y cajas para pianos.

Ejemplares examinados. MÉXICO. **Estado de México**: Aculco de Espinosa, Bosque Ñado, 10 km antes de Aculco de Espinosa, *Matuda 28731* (ENCB); Almoloya de Juárez, km 11 de la carretera Toluca–Valle de Bravo, *Estrada 346* (ENCB); Amecameca, San Antonio Zoyatzingo, *Ávila s.n.* (ENCB); 1 km al NE de Santo Tomás Atzingo, *Cervantes 181* (ENCB); 3 km al SW de San Antonio Zoyatzingo, *Pineda 528* (ENCB); Cerro Sacromonte, *Rzedowski 26695a* (ENCB); Capulhuac, Cerro Xiloxi, 1 km al W de San Miguel Almaya, *Rodríguez s.n.* (ENCB); Coacalco, 6 km al S de Coacalco, Sierra de Guadalupe, *Rzedowski 30777* (ENCB); Chalco, Ladera E del Cerro La Tijera, 1 km al SE de Santa Ana, *Pineda 393* (ENCB); Chicoloapan, 4 km al E de Coatepec, *Román 311* (ENCB); El Oro de Hidalgo, El Oro de Hidalgo, *Matuda 26420, 28647* (CODAGEM); cercanías del Oro, *Matuda 28624* (ENCB); Ecatepec de Morelos, 6 km al N de Santa Clara, *Ramírez 127* (ENCB); Huixquilucan, Fraccionamiento La Herradura, *Domínguez s.n.* (ENCB); Dos Ríos, *Matuda 28405, 28406* (ENCB); alrededores de Dos Ríos, *Román 327* (ENCB); Ixtapaluca, Río Frío, *García 92* (ENCB); km 42 carretera México–Puebla, *Hernández 64* (ENCB); Jilotepec, Denxi, *Martínez 67* (IZTA); Jilotepec, *Matuda 26674* (CODAGEM, ENCB); Cerro de Jilotepec, *Matuda 29052* (ENCB); en Cerro de San Bartolo, *Matuda 29065* (ENCB); Jocotitlán, Cerro de Jocotitlán, *Matuda 30238* (ENCB); Otumba de Gómez Farías, 15 km al NE de Texcoco, *Ochoa 40* (ENCB); Cerro Cuixi al E de Santa Bárbara, *Rzedowski 16889* (ENCB); Otzoloapan, Cerro de Pinal, *Matuda 31754, 31870* (CODAGEM); Ozumba de Alzate, al S de Ozumba de Alzate, *COTECOCA 15036* (ENCB); Tenango de Tepopula, San Luis Aculco de Espinosa, *Hinton 115, 117* (ENCB); 3 km al W de Tenango de Tepopula, *Pineda 731* (ENCB); San Martín de las Pirámides, Cumbre del Cerro Gordo, *Rzedowski 18801* (ENCB); Temascaltepec de González, Cieneguillas, 14 km al W de Temascaltepec de González, *Moreno 185* (CHAPA, ENCB); Temascalapa, Cerro Gordo, *Castilla & Tejero 634* (ENCB, IZTA); Tepetlaoxtoc, 18 km al E de Texcoco, por la carretera a Calpulalpan, *De la Cruz 15* (ENCB); 14 km al E de Texcoco, *Koch 75134* (ENCB); Tepotzotlán, 3 km al W de Magú, *Mendiola 188* (ENCB); parte alta de la Sierra de Alcaparrosa, cerca de la estación de microondas, *Rzedowski 29936* (CHAPA, ENCB); Texcoco, 20 km al NE de Texcoco, *Cruz 1834* (ENCB); Cerro Tetzahuitl, *Chávez 2233* (ENCB); 24 km al E de Texcoco, *García s.n.* (CHAPA); 19 km al E de Texcoco, *Koch 75134* (ENCB); Tlalmanalco, *Medellín s.n.* (ENCB); Tlazala de Fabela, 4 km al E de Santiago Tlazala, *Jiménez s.n.* (ENCB); 7 km al E de Santiago Tlazala, *Luna s.n.* (ENCB); Cañada de Onofre, *Román 279* (ENCB); Toluca, Centro Ceremonial Toluca, *Cuellar s.n.* (ENCB); Valle de Bravo, ladera E del Cerro Gordo, *Muller 9107* (ENCB); Villa del Carbón, Predio Piedra Azul, *Ávila s.n.* (ENCB); San Jerónimo, *Matuda 29014* (ENCB); Cerro La Bufa, *Matuda 29735* (ENCB); Villa Nicolás Romero, 3 km al NW de Cahuacán, *Acosa 6100* (CODAGEM); 5 km al SW de Cahuacán, *González 875* (ENCB); 4 km al E de Santiago Tlazala, *Jiménez s.n.* (ENCB); 7 km al E de Santiago Tlazala, *Luna 2500* (ENCB); 2 km de Cahuacán, *Mortecinos 200* (ENCB); 2 km al NW de Cahuacán, *Rzedowski 33758* (ENCB).

17. Quercus dysophylla Bentham, Pl. Hartw. 55. 1840. TIPO: México. Huasca: *Hartweg 421* (holotipo, K!).

Quercus esperanzae Trel., Mem. Natl. Acad. Sci. 20: 132, pl. 248. 1924. Syn. nov. TIPO: México. Esperanza, *Purpus 5332* (NY!).

Quercus fournieri Trel., Mem. Natl. Acad. Sci. 20: 177, pl. 357. 1924. Syn. nov. TIPO: México. Cofre de Perote, *Hahn 255* (P!).

Quercus hahnii Trel., Mem. Natl. Acad. Sci. 20: 131, pl. 247. 1924. TIPO: México. Cajalpa, cerca de Toluca, *Hahn 347* (P!).

Árbol de 5–20 m de alto, ramillas de 1–3 mm diám., estriadas, glabrescentes, el indumento se extiende a los pecíolos y nervadura central, formado de tricomas estrellados estipitados, de color castaño-rojizo; lenticelas hasta de 1 mm de largo, más claras que el tallo; yemas de 2–5 mm de largo, ovoides, de color café claro, con el ápice redondeado y los bordes largamente ciliados; estípulas caedizas, lineares, de 4–9 mm de largo, pubescentes en toda su superficie; hojas maduras gruesas y coriáceas, ovadas, lanceoladas o elípticas, lámina (3–)5–15(–17) × (1–)2–5(–6) cm, ápice obtuso o agudo, mucronado o aristado, aristas de hasta 2 mm de largo, base redondeada o cordada, a veces asimétrica, borde revoluto, entero u ondulado, a veces con algunos dientes, con 0 a 13 aristas en cada lado, de hasta 2 mm de largo; nervaduras de 9 a 15 en cada lado, rectas o algo curvas, se bifurcan

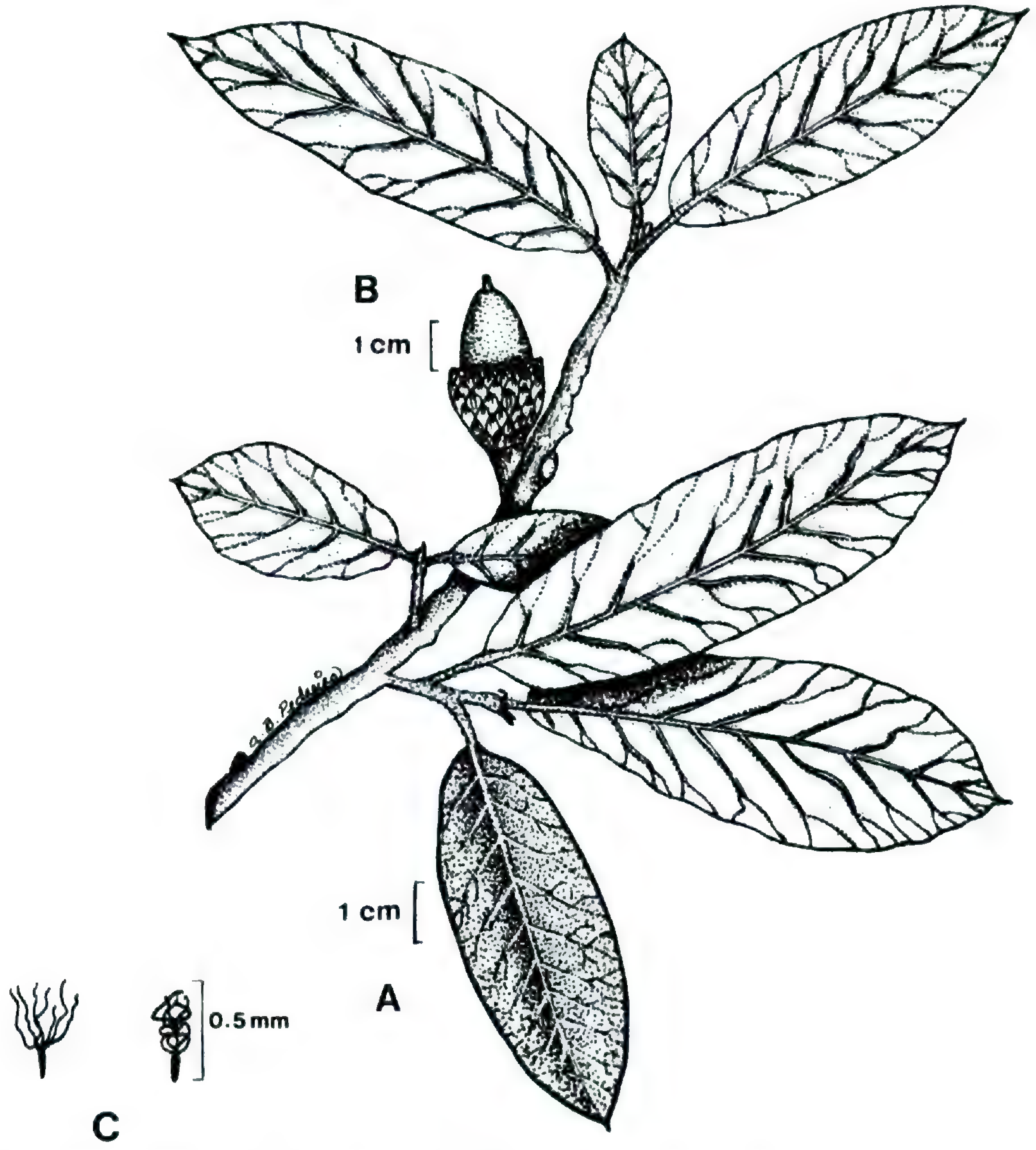

Figura 17. *Quercus dysophylla.*—A. Rama. —B. Fruto. —C. Tricomas. (*Romero 1.*)

en el tercio distal o cerca del margen; haz verde pálido, glabro, con tricomas estrellados, estipitados, dispersos sobre la lámina, abundantes sobre la nervadura central, nervaduras impresas; envés con pubescencia amarilla, formada por tricomas estrellados, estipitados, y por escasos o abundantes tricomas simples glandulares que dejan ver la epidermis ampulosa, nervaduras elevadas; pecíolos de (2–)4–7(–12) mm de largo, de 1–2 mm diám., densamente pubescentes, se ennegrecen con la edad; flores desconocidas; fruto solitario o en grupos de dos, sésiles o en pedúnculos de 1–2 mm de largo, con lenticelas claras; cúpula turbinada, de 10–12 mm diám., de 8–12 mm de alto, borde recto, a veces involuto; escamas no engrosadas en la base, no adpresas, excepto las superiores, canescentes, ápice obtuso, márgenes más obscuros; bellota ovoide, pared interna de pericarpo lanosa, de 12–17 mm de largo, de 10–11 mm diám., de color castaño claro, incluída la mitad de su largo en la cúpula. Figura 17.

Reconocimiento. *Quercus dysophylla* se reconoce por sus hojas lanceoladas o elípticas, con el borde entero y aristado, envés con pubescencia amarilla y epidermis ampulosa; puede confundirse con *Q. crassifolia* y *Q. hintonii. Quercus crassifolia* se reconoce por sus hojas obovadas, dentadas, aristadas con el envés lanoso amarillo, anaranjado o café, y epidermis ampulosa. *Quercus hintonii* se distingue porque el envés de sus hojas posee epidermis lisa y las ramas de los tricomas estrellados son más largas que las especies anteriores.

Distribución y hábitat. México en los estados de Distrito Federal, Guanajuato, Hidalgo, Estado de México, Michoacán, San Luis Potosí, Tlaxcala y Veracruz. Se le encuentra en bosques de *Quercus, Pinus–Quercus,* bosque mesófilo de montaña y bosque de *Pinus* perturbado, y se asocia con *Quercus rugosa* y *Q. castanea,* en altitudes de 2490–2850 m.

Fenología. Florece en marzo y abril y fructifica en septiembre y octubre.

Nombres populares y usos. Encino, laurelillo. Bello y Labat (1987) señalan que se utiliza como leña y postes de cercas.

Ejemplares examinados. MÉXICO. **Estado de México**: Amecameca, Alcansi, *Vela & Mancera s.n.* (INIF); Amecameca, *Vela & Mancera s.n.* (IZTA); Cañada al NE de Chalma, *Rzedowski 27199* (ENCB); Donato Guerra, 2 km del entronque de Donato Guerra, carretera Toluca–Valle de Bravo, *Rojas & Romero 3246* (IZTA); Huixquilucan, 2 km al S de Huixquilucan, *Espinosa 713* (ENCB); alrededores de Huixquilucan, *Román 332* (IZTA); Tepotzotlán, Sierra de Alcaparrosa, *Núñez 1677* (ENCB); parte alta de la Sierra de Alcaparrosa, *Rzedowski 31264* (ENCB); Timilpan, San Andrés Timilpan, *Camacho 357, 360, 241* (IZTA); Tlazala de Fabela, 4 km al E de Santiago Tlazala, *Jiménez 141* (ENCB); Villa del Carbón, Villa del Carbón, *Ramos 1* (IZTA); Villa Nicolás Romero, Villa Nicolás Romero, *Jiménez s.n.* (ENCB); 2 km al NW de Cahuacán, *Rzedowski 33757* (ENCB); 1 km al NE de Cahuacán, *Tirado s.n.* (ENCB).

18. Quercus elliptica Née, Anales Ci. Nat. 3: 278. 1801. TIPO: México. Hidalgo: Ixmiquilpan y Zimapán, *Née s.n.* (P).

Árbol de 8–15 m de alto, con el tronco de 15–70 cm diám., corteza gris obscura; ramillas densamente pubescentes, de 2–3 mm diám., al principio de color amarillo, después se ennegrecen, el indumento formado por tricomas estrellados unos largos y otros cortos, erectos; lenticelas escasas cubiertas por la pubescencia, de hasta 0.5 mm de largo; yemas de 2–4 mm de largo, ovoides, de color castaño obscuro; estípulas de 7–8 mm, oblanceoladas, ciliadas, principalmente en ápice y base, membranosas, escariosas, decíduas; hojas jóvenes con el haz y envés cubiertos de pequeños pelos estrellados, los de la nervadura central más largos, y pelos simples glandulares color ámbar; hojas maduras rígidas, coriáceas, elípticas, lanceoladas u oblanceoladas, lámina (2.1–)4.5–12 × (1.8–)3–5(–6.5) cm, ápice obtuso, agudo o emarginado, cuando es agudo a veces con arista de hasta 2 mm de largo, base redondeada, cordada o auriculada, borde entero, engrosado, cartilaginoso, ligeramente revoluto; nervaduras de 8 a 16 en cada lado, se ramifican en el borde, forman arcos interconectados; haz verde pálido, lustroso, casi glabro, con pequeños pelos muy dispersos, en la base de la nervadura central se agrupan pelos con rayos más largos, nervaduras impresas o ligeramente elevadas; envés glabro, a veces con pelos estrellados dispersos sobre la lámina, con aproximadamente 6 rayos cortos extendidos, en las axilas de las nervaduras son más largos, nervaduras elevadas, pálidas, gruesas, epidermis ligeramente ampulosa, papilosa; pecíolos de (3–)4–7 mm de largo, de 1–1.5 mm diám., densamente pubescentes; amentos masculinos de 5–9 cm de largo, de muchas flores en posición alterna, flores sésiles, perianto de 2–4 mm diám., de 1.5–2 mm de largo, lóbulos ciliados, 4 a 7 estambres, anteras oblongo-elipsoidales, de 1–1.5 mm de largo, glabras, filamentos de 1–2 mm de largo, raquis muy pubescente; flores femeninas solitarias, en pares o en grupos de 4 a 5 sobre un pedúnculo pubescente de 1–1.5 cm de largo; frutos de 1 a 3, sobre un pedúnculo de 2–3 mm de largo; cúpula pateliforme, de 3–4 × 14–15 mm diám., escamas triangulares, no engrosadas en la base, ápice obtuso, pubescente, bordes más obscuros; bellota ancha, pared interna del pericarpo lanosa, ovoide de 13–15 × 14–15 mm diám., incluída en la cúpula menos de una tercera parte. Figura 18.

Discusión. *Quercus elliptica* se reconoce por sus hojas elípticas, ápice aristado y envés glabrescente.

Distribución y hábitat. En México en los estados de Guerrero, Jalisco, Estado de México, Michoacán, Nayarit, Oaxaca, Sinaloa y Veracruz, también en América Central. Habita en bosques de *Pinus–Quercus* y de galería, en altitudes de 1500–1900 m.

Fenología. Florece de febrero a marzo y fructifica en octubre.

Nombres populares y usos. Encino cucharita, encino tapahuite, encino nanche, encino colorado, encino laurel, encino cáscara. Su madera se usa como leña y para elaborar carbón (González, 1986), también para bancos, muebles rústicos, mangos, cabos de herramienta, vigas de construcción y postes.

Ejemplares examinados. MÉXICO. **Estado de México**: Tejupilco, Paso del Jate, Parque Cinegético Nanchititla, *Abundiz 525, 536* (IZTA); Reserva Cinegética de Nanchititla, *Frutis 1966* (IZTA); en falda N del cerro, *Matuda 31544* (CODAGEM); km 23 El Corupo–Nanchititla, *Rojas & Romero 3956* (IZTA); km 12 El Corupo–Nanchititla, *Rojas & Romero 3957* (IZTA); 2 km al NW de Nanchititla, *Rzedowski 22116* (ENCB); Nanchititla, alrededores de la población, *Rzedowski 30303, 30309* (ENCB).

19. Quercus hintonii E. F. Warburg, Bull. Misc. Inform.: 91. 1939. TIPO: México. Estado de México: Temascaltepec de González, Nanchititla, *Hinton 6359* (holotipo, K!).

Quercus apiophylla E. F. Warb., Bull. Misc. Inform.: 95. 1939. TIPO: México. Estado de México: Temascaltepec de González, Berros, *Hinton 6568* (holotipo, K!).

Quercus ochroestes E. F. Warb., Bull. Misc. Inform.: 94. 1939. TIPO: México. Estado de México: Temascaltepec de González, Mina de Agua, *Hinton 6576* (holotipo, K!).

Quercus sagata E. F. Warb., Bull. Misc. Inform.: 90. 1939. TIPO: México. Estado de México: Distrito de Te-

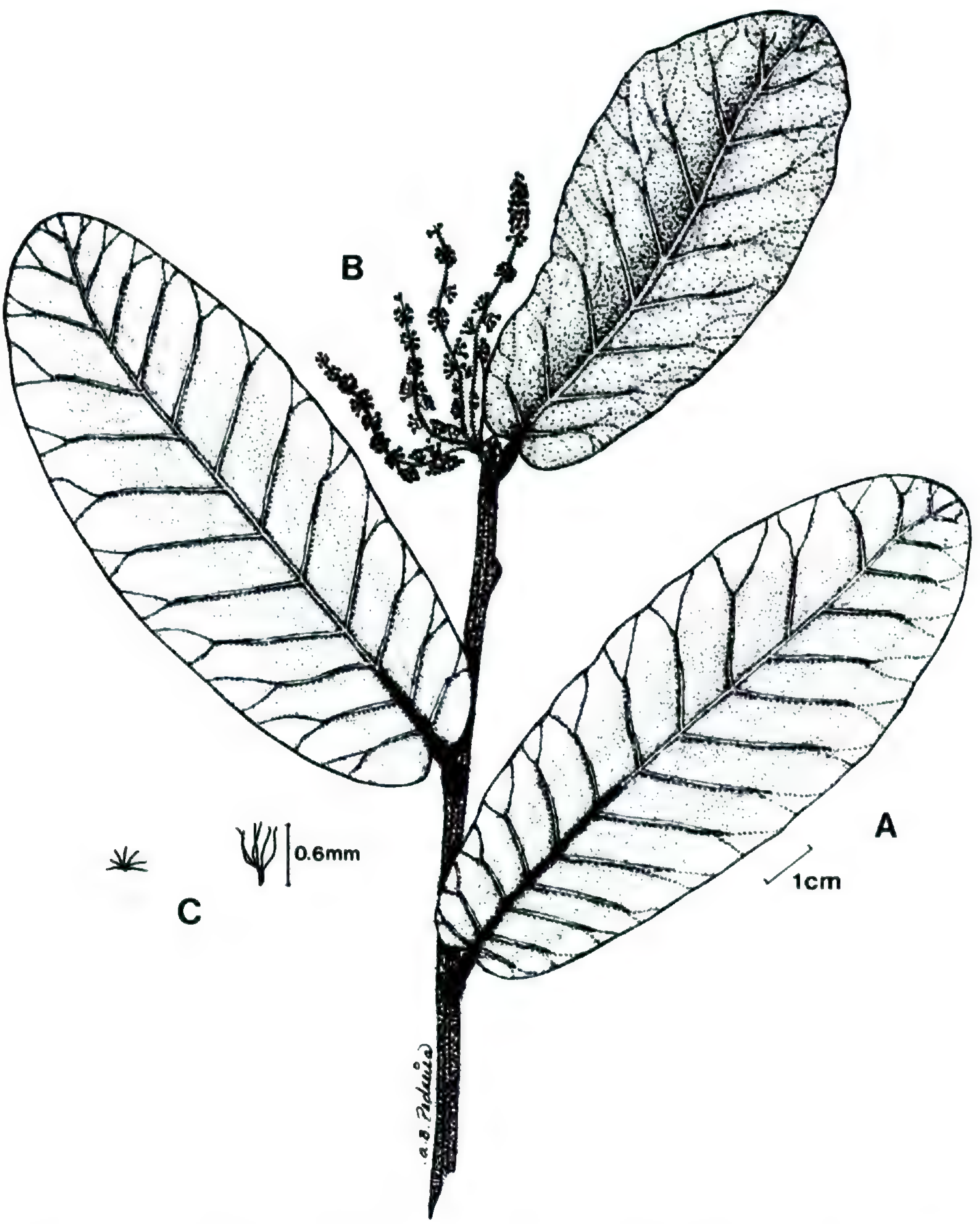

Figura 18. *Quercus elliptica.*—A. Rama. —B. Inflorescencia masculina. —C. Tricomas. (*Romero 3991.*)

mascaltepec de González, Cuentla, *Hinton 6577* (fotografía del holotipo, K!).

Árbol caducifolio, hasta de 15 m de alto; tronco de 30–50 cm diám., corteza con placas cuadrangulares, en individuos muy jóvenes ésta es rugosa; ramillas jóvenes de 1–4 mm diám., con abundante pubescencia blanco-amarillenta, formada de tricomas estrellados, que se reduce y ennegrece con el tiempo; lenticelas blancas, de 0.5–1 mm, más notorias en ramas viejas; yemas ovoides, de color castaño obscuro, de 1–8 mm de largo, con escamas coriáceas y pilosas; estípulas oblanceoladas, de 9–13 mm de largo, membranosas, pilosas en márgenes y base, decíduas; hojas jóvenes con abundante pubescencia rojiza que cambia a amarillo en la madurez; hojas maduras coriáceas, lanceoladas, ovado-lanceoladas, obovadas o elípticas, lámina 5–21 × 3–10 cm, ápice aristado, corto a largamente acuminado, base obtusa, redondeada, cordada o aguda, con frecuencia asimétrica, borde aristado, dentado, a veces entero, revoluto, hasta con 7 aristas en cada lado, es frecuente que éstas se presenten en un sólo lado; las nervaduras se prolongan hasta las aristas, las primeras de 6 a 14 en cada lado, rectas o ligeramente arqueadas, ascendentes, ramificandose en el borde; haz verde claro, lustroso, glabro excepto en la base y en la nervadura central, en hojas inmaduras es rojizo a verde obscuro, con abundante pubescencia formada por tricomas estrellados y simples glandulares, con la madurez la pubescen-

cia disminuye en cantidad y cambia de rojiza a blanco-amarillenta; nervadura central a veces algo elevada, nervaduras primarias y secundarias impresas; envés lanoso tomentoso, con tricomas estrellados de aproximadamente 1.5 mm de largo, con las ramas entrelazadas, epidermis lisa, con abundantes tricomas simples glandulares, de color ámbar, el tomento cambia de blanco en hojas jóvenes, a amarillo en las maduras, nervaduras conspicuamente elevadas; pecíolo de 0.7–2.9 × 1–2 mm, lanoso tomentoso, con frecuencia más ancho en la base; amentos masculinos de 3–10 cm de largo con muchas flores, raquis con abundante pubescencia, perianto pubescente de 1–2 mm de largo y de 2 o 3 mm diám., amarillento, con frecuencia los bordes son rojos, estambres 6 o 7, exertos, anteras oblongas, glabras, apendiculadas, de 1–1.5 × 1 mm, con frecuencia rojizas, filamentos hasta de 2 mm de largo; amentos femeninos de 1–14 cm de largo, con 1 a 6 flores, raquis pubescente; perianto de 2 × 1.5 mm, amarillento; estigmas 3 o 4, espatulados, de color rojo obscuro; frutos 1 a 4 en pedúnculos de 6–7.5 mm; cúpula poculiforme a pateliforme, de 10–14 mm diám., de 4–7 mm de alto, escamas laxas con ápices de color castaño, pubescentes; bellota globosa a comprimida, pared interna del pericarpo lanosa, de 6–15 mm de largo, de 9–13 mm diám. con el ápice plano a umbonado. Figura 19.

Discusión. *Quercus hintonii* se reconoce por sus hojas generalmente lanceoladas, aristadas, con el envés densamente tomentoso y epidermis lisa. *Q. hintonii* muestra similitud con *Q. crassifolia* y *Q. dysophylla* (ver descripción de *Q. crassifolia*).

Distribución y hábitat. En México en el Estado de México. En bosques de *Quercus–Pinus*, se asocia con *Quercus magnoliifolia*, *Pinus oocarpa*, *P. pringlei*, *Clethra mexicana* y *Juniperus flaccida*, en altitudes de 1300–1950 m.

Fenología. Florece en marzo y los frutos maduran en junio a agosto.

Nombres populares y usos. Encino prieto.

Su madera es empleada localmente para la elaboración de mangos de herramientas, vigas, postes de cerca, bancos rústicos y leña. Podría utilizarse para fabricar duelas de parquet, lambrín, muebles, durmientes, pilotes para minas y barricas (Arcia, 1979).

Ejemplares examinados. MÉXICO. **Estado de México**: Amatepec, cercanías de Amatepec, *Matuda & col. 29823* (CODAGEM); Clachichilpan, 7 km al NE, *Pineda 1048* (INIF); 4 km al S de Amatepec, *Pineda 1052* (INIF); San Simón de Guerrero, km 83 Toluca–San Diego Cuentla, *Rojas, Romero & Aguilar 3218* (ENCB, IZTA); Mina de Agua, *Rojas & Romero 3605* (ENCB, IZTA); Los Berros Cuentla, *Rojas & Romero 3606* (ENCB, IZTA); Sultepec, km 25 carretera a San Miguel Totolmoloya, *Torres 575* (IZTA); Tejupilco, Cerro de Nanchititla, *García s.n.* (IZTA); alrededores de la población de Tejupilco, *Rzedowski 30302* (INIF); 5 km al SW de Nanchititla, *González 5026, 5049* (MEXU); Peña Bonita, *González 5399, 5444, 5447* (MEXU); Potrero Chico, *González 5436, 5438* (MEXU); Reserva Ecológica de Nanchititla, *Jiménez 318* (IZTA); 5 km al NE de Palos Prietos, *Pineda 1044* (INIF); Los Cuervos, *Rojas & Romero 3604* (ENCB, IZTA); Temascaltepec de González, Chorrera, *Hinton 6199* (ENCB); Pantoja, *Hinton 6225* (ENCB); km 70 carretera Federal 134, *Rojas & Romero 3400* (ENCB, IZTA); 5 km al SW de Temascaltepec de González, sobre la carretera a Tejupilco, *Rzedowski 20829* (INIF); Tlatlaya, Tlatlaya y cercanías, *Matuda & col. 29825, 29827, 31588* (CODAGEM).

20. Quercus laurina Humboldt & Bonpland, Pl. Aequinoct. 2: 32, pl. 80. 1809. TIPO: México. Hidalgo: Cerro de las Navajas, cercanías de Morán, *Bonpland 4143* (isotipo, B!).

Quercus barbinervis Benth., Pl. Hartw. 56. 1840. TIPO: México. Hidalgo: Real del Monte, *Hartweg 427* (K).
Quercus bourgaei Oersted ex Trelease, Mem. Natl. Acad. Sci. 20: 168, pl. 366. 1924. TIPO: México. San Nicolás, Valle de México, *Bourgeau 1013* (B).
Quercus lanceolata Humb. & Bonpl., Pl. Aequinoct. 2: 34, pl. 81. 1809. TIPO: México. Morán a Santa Rosa, *Bonpland s.n.* (B).
Quercus caeruleocarpa Trel., Mem. Natl. Acad. Sci. 20: 163, pl. 321. 1924. TIPO: México. Distrito Federal: Contreras, 9 Sep. 1906, *Endlich 1365 a* (B).

Árbol de 10–30 m de alto, tronco de 50 cm diám. o más, corteza con grietas poco profundas y piezas chicas, de color gris obscuro; ramillas de color gris, de 1–2.5 cm diám., pubescentes al principio, después glabrescentes, pubescencia de tricomas estrellados pequeños; lenticelas menores de 0.5–3 mm de largo, de color claro u obscuro; yemas de 1.5–4 mm de largo, ovoides, agudas, de color castaño, escamas gruesas con el margen apical ciliado; estípulas de 3–6 mm de largo, oblanceoladas o subagudas, escariosas, membranosas, decíduas; hojas jóvenes con pubescencia formada por tricomas estrellados pequeños y simples dispersos en haz y envés, con el tiempo ésta se reduce a las nervaduras central y primarias; hojas maduras rígidas, coriáceas, lustrosas, lanceoladas o elíptico-oblanceoladas, lámina (2–)5–11(–15.5) × 1.5–4(–6.5) cm, ápice agudo o acuminado y por lo general aristado, base redondeada, cordada, atenuada o cordada, borde entero o dentado, plano o revoluto, a veces ondulado, engrosado, con 1 a 5 aristas de cada lado, a veces se presentan sólo de un lado de la hoja, distribuidas en el tercio superior; nervaduras primarias de 4 a 12 en cada lado, rectas o ligeramente arqueadas, ascendentes, se ramifican antes del margen; haz verde lustroso, todas las nervaduras pálidas y elevadas, nervadura central pu-

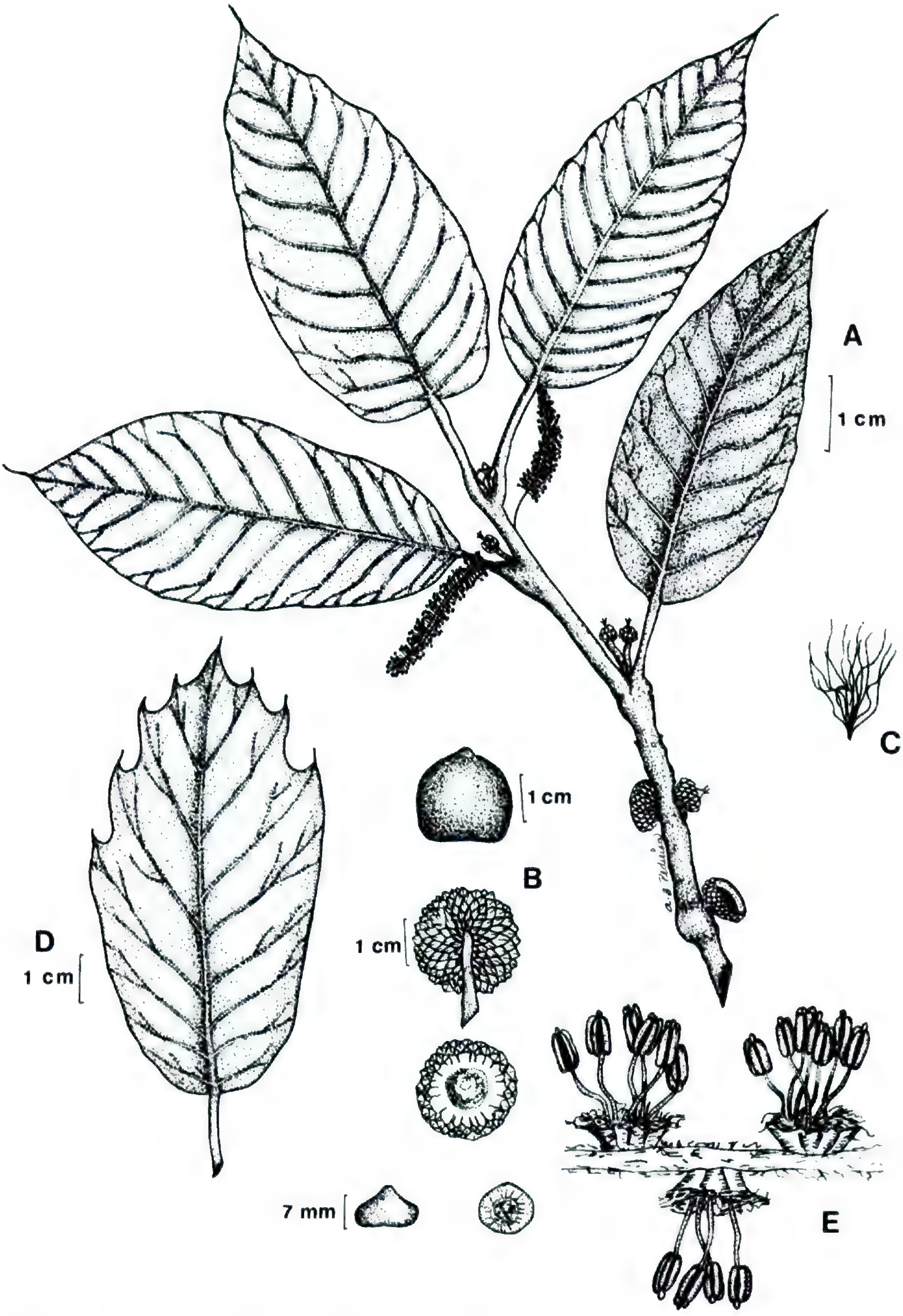

Figura 19. *Quercus hintonii*.—A. Rama. —B. Fruto. —C. Tricoma. —D. Hoja. —E. Flores masculinas. (*Romero 3604*.)

bescente en su base; envés lustroso, amarillo o a veces más pálido que el haz, pubescencia de tricomas estrellados estipitados, restringida por lo general a las axilas de las nervaduras primarias, donde se observan tricomas simples, blancos y escasos tricomas glandulares de color ámbar, epidermis papilosa, nervaduras elevadas; pecíolos de (2–) 5–15(–22) mm de largo, de 0.5–1.5 mm diám., finamente pubescentes, glabrescentes; amentos masculinos de 3.5–4.5 cm de largo, raquis negro con

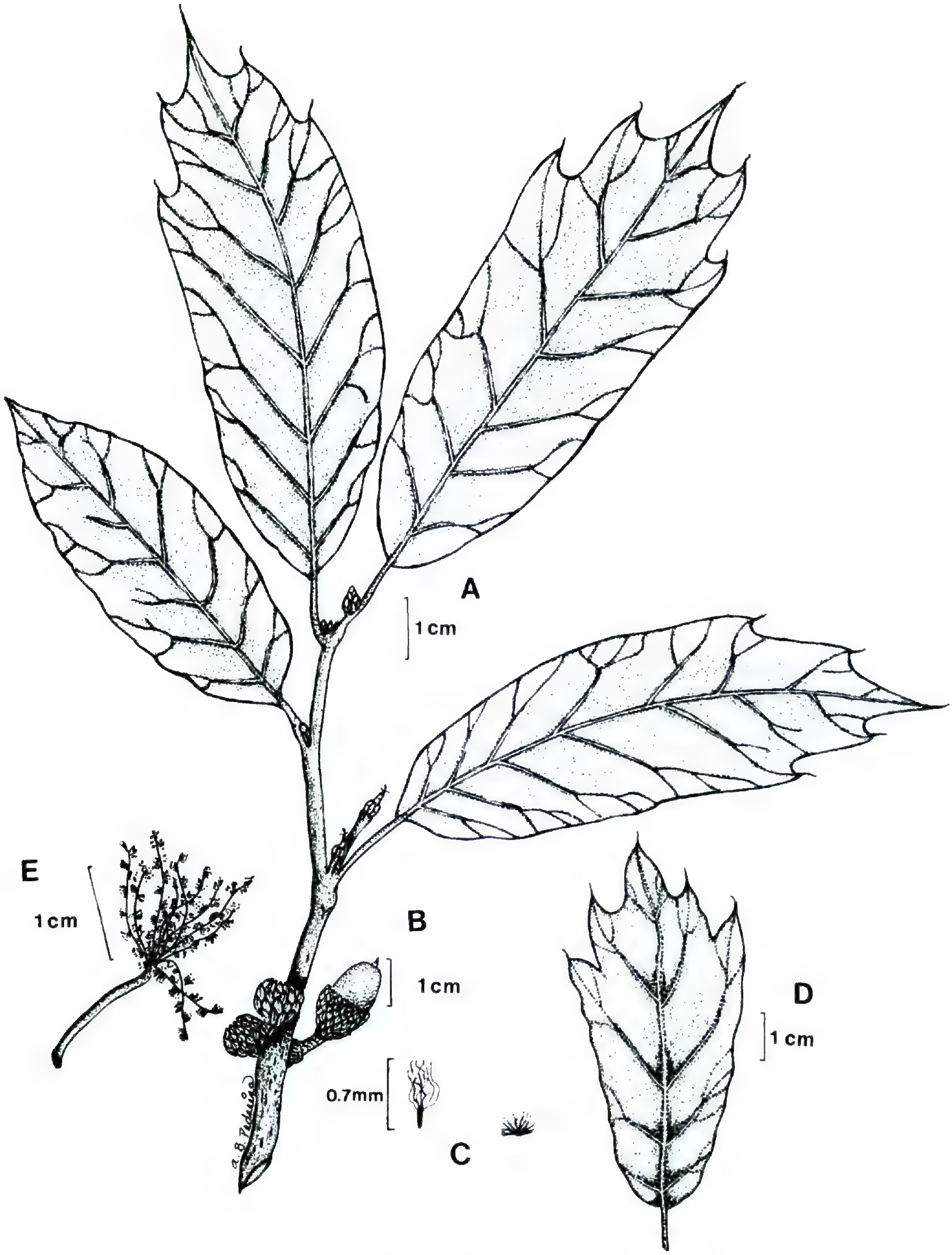

Figura 20. *Quercus laurina.*—A. Rama. —B. Fruto. —C. Tricomas. —D. Hoja. —E. Inflorescencias masculinas. (A–C: *Torres 1468*; D, E: *Romero 3321.*)

tricomas largos, perianto de 2–3 mm diám., con los lóbulos largamente ciliados, anteras de 1.5 mm de largo, filamentos de 1 mm de largo; fruto anual o bianual, solitario, en pares o en grupos de 3, sésiles o en pedúnculos de 3–12 mm de largo; cúpula hemisférica, de 10–15 mm diám., escamas leñosas, no engrosadas en la base, pubescentes, de ápice obtuso; bellota ovoide, pared del pericarpo lanosa, de 7–19 mm de largo, de 7–12 mm diám., incluída un tercio de su largo en la cúpula. Figura 20.

Discusión. *Quercus laurina* se reconoce por sus

hojas aristadas, el envés con pubescencia restringida a las axilas de las nervaduras. Esta especie posee similitud morfológica con *Q. affinis* y se distingue por poseer yemas florales de forma conoidal, base de las hojas cuneada y nervaduras planas; mientras que *Q. laurina* posee las yemas ovoides, base de las hojas atenuada o redondeada y nervaduras elevadas.

Distribución y hábitat. En México en los estados de Distrito Federal, Guanajuato, Guerrero, Hidalgo, Jalisco, Estado de México, Michoacán, Morelos, Puebla, Querétaro, Oaxaca, Tlaxcala y Zacatecas. En bosques de *Pinus–Quercus*, *Pinus–Abies*, bosque mesófilo de montaña y encinares perturbados, en altitudes de 2240–3150 m.

Fenología. Florece en abril y fructifica de junio a octubre.

Nombres populares y usos. Chilillo, encino colorado, atlualpitzahul, encino blanco, encino laurelillo, encino roble, encino xicatahua, tesmolera, encino hoja angosta, huitzalacate, encino prieto, encino uricua, encino chilillo.

Se utiliza para bancos, muebles rústicos, cabos de herramienta, vigas de construcción, papel Kraft y fabricación de chapa (González, 1986) y como leña.

Ejemplares examinados. MÉXICO. **Estado de México**: Acambay, cerro Detiña, *Estrada 1468* (IZTA); Muyteje, *Quintero & Rojas 18, 22* (IZTA); Amanalco de Becerra, 5 km al NW de Agua Bendita, *Pineda 1347* (INIF); Amecameca, barrancas de San Antonio Zoyatzingo, *Ern 159* (ENCB); Alcansi, *Vela & Mancera s.n.* (ENCB); 1 km al E de San Antonio Zoyatzingo, *Rzedowski 26432* (ENCB); 1 km al E de San Antonio, base del Ixtaccihuatl, *Xelhuantzi 5081* (INIF); Atizapán, cumbre del Cerro Chilluca, *Rzedowski 32611* (ENCB); Atlautla, Tecomazusco, camino de Atlautla, al paraje de Santa Teresa, *Hernández 40* (INIF); Capulhuac, Cerro Xiloxi, 1 km al W de San Miguel Almaya, *Rodríguez s.n.* (ENCB); Coacalco, 5 km al S de Coacalco, vertiente N de la Sierra de Guadalupe, *Rzedowski 30768* (ENCB); Sierra de Guadalupe, 6 km al S de Coacalco, *Rzedowski 30774* (ENCB); Coatepec de Harinas, 15 km al N de Coatepec Harinas, sobre el camino a Las Lágrimas, *Hernández s.n.* (ENCB); San Francisco Coatepec, *Ortega 42* (ENCB); 5 km al E de Coatepec, *Román 315* (ENCB); Chalco, cerca de la colonia Agrícola Manuel Ávila Camacho, *Cabrera s.n.* (ENCB); Chicoloapan, 5 km al E de Coatepec, *Román 311* (ENCB); El Oro de Hidalgo, La Cima, *Pérez 19* (IZTA); La Cima, *Valdés 1* (IZTA); Huixquilucan, Salazar, *Matuda 28101* (ENCB); Ixtapaluca, Estación Experimental de Enseñanza e Investigación de Zoquiapan, *Magaña 1160* (ENCB); 1 km al NE de Llano Grande, *Rivas & Campos 13* (ENCB); 6 km al SW de Río Frío, *Roe, Roe & Scott 1440* (ENCB); Jiquipilco, vertiente W de la Sierra de las Cruces, *Álvarez 8, 15* (IZTA); km 15 carretera Jiquipilco–Villa del Carbón, *Romero & Rojas 3176* (IZTA); Jilotepec, San Bartolo, *Matuda & col. 29063* (ENCB); Santa Ana Jilotzingo, 3 km al E de San Luis Ayucan, *Fernández 36* (ENCB); Lerma, Santa María Tlalmimilolpan, cerca de Lerma, *Franco 63* (ENCB); cerca de Salazar, *Villanueva s.n.* (ENCB); Naucalpan de Juárez, Villa Alpina, *Corona s.n.* (ENCB); El Guarda, *Herrera 191* (ENCB); Santiago Tepatlaxco, *Jiménez 132* (IZTA); Los Remedios, *Madrigal 74* (INIF); San Francisco Chimalpa, *Ruiz 33* (INIF); Ocuilan de Arteaga de Arteaga, km 18 terracería Ocuilan de Arteaga–Cuernavaca, *Castañeda, Lugo & Trejo 13* (IZTA); San Martín de las Pirámides, Cumbre del Cerro Gordo, *Rzedowski 18810* (ENCB); Sultepec, La Cieneguilla, *Rodríguez 163* (ENCB); San Miguel Totolmoloya, *Torres 302* (IZTA); Temascalapa, Cerro Gordo, *Castilla & Tejero s.n.* (ENCB); Temascaltepec de González, Comunal de Tequisquiapan, *Huerta, Ramos & col. 8* (IZTA); Comunal de Tequisquiapan, *Huerta T-8* (ENCB); Teotihuacán, Cerro Gordo al N de Teotihuacán, *Espinosa 635a* (ENCB); Texcoco, 24 km al E de Texcoco, sobre brecha rumbo a Tlaloc, *García s.n.* (ENCB); 8 km al SE de Tequesquinahuac, *Perino 3137* (ENCB); Cañada al SE de San Pablo Ixayoc, *Rzedowski 32741* (CHAPA, ENCB); Santa Catarina del Monte, *Ventura 1123* (INIF); Timilpan, Sierra de San Andrés, *Camacho 248* (IZTA); Tlalmanalco, San Rafael, *Madrigal s.n.* (INIF); 4 km al E de San Rafael, *Magaña 1057* (INIF); Tlalmanalco, *Medellín 227* (INIF); 3 km al S de San Rafael, *Ramírez 406* (ENCB); Villa del Carbón, El Plan, *González s.n.* (IZTA); El Gato San Jerónimo, *Rojas & Romero 3168* (IZTA); Villa Nicolás Romero, Transfiguración, *Ocaña s.n.* (IZTA); Zacualpan, cerro La Corona, *Matuda 30324* (CODAGEM).

21. Quercus mexicana Humboldt & Bonpland, Pl. Aequinoct. II: 35, pl. 82. 1809. TIPO: México. Guanajuato: Santa Rosa, *Bonpland 4218* (B).

Quercus rugulosa Mart. & Gal., Bull. Acad. Roy. Sci. Bruxelles, Vol. 10, pt. II: 209. 1843. TIPO: México. San Pedro y San Pablo, cerca de Real del Monte, *Galeotti 116* (BR).

Árbol de 3–15 m de alto, corteza gris; ramillas de 1.5–2 mm diám., al principio con pubescencia formada de tricomas estrellados, pronto glabras, corteza gris, con lenticelas menores de 0.5–2(–3) mm de largo, casi del mismo color que la corteza; yemas de (1–)2–3(–6) mm de largo, ovoides, ápice agudo, de color castaño, escamas pubescentes en sus márgenes; estípulas de 3–5 mm de largo, escariosas, lineares, caedizas, algunas persistentes por un tiempo cerca de las yemas apicales; hojas jóvenes del mismo color que las adultas; haz con el indumento formado de tricomas estrellados muy pequeños dispersos, envés con tricomas estrellados dispersos; hojas maduras decíduas, elípticas, lanceoladas u oblongas, coriáceas, lámina (2–)3–9(–12) × (0.9–)1.5–3.5(–4.2) cm, ápice agudo, subagudo o redondeado, con una arista de hasta 2.5 mm de largo, base ligeramente revoluto, engrosado, cartilaginoso, borde entero; nervaduras de 6 a 12 en cada lado, ascendentes, casi rectas, se bifurcan en el ápice; haz verde obscuro, con algunos tricomas estrellados dispersos en la base de la hoja y en la

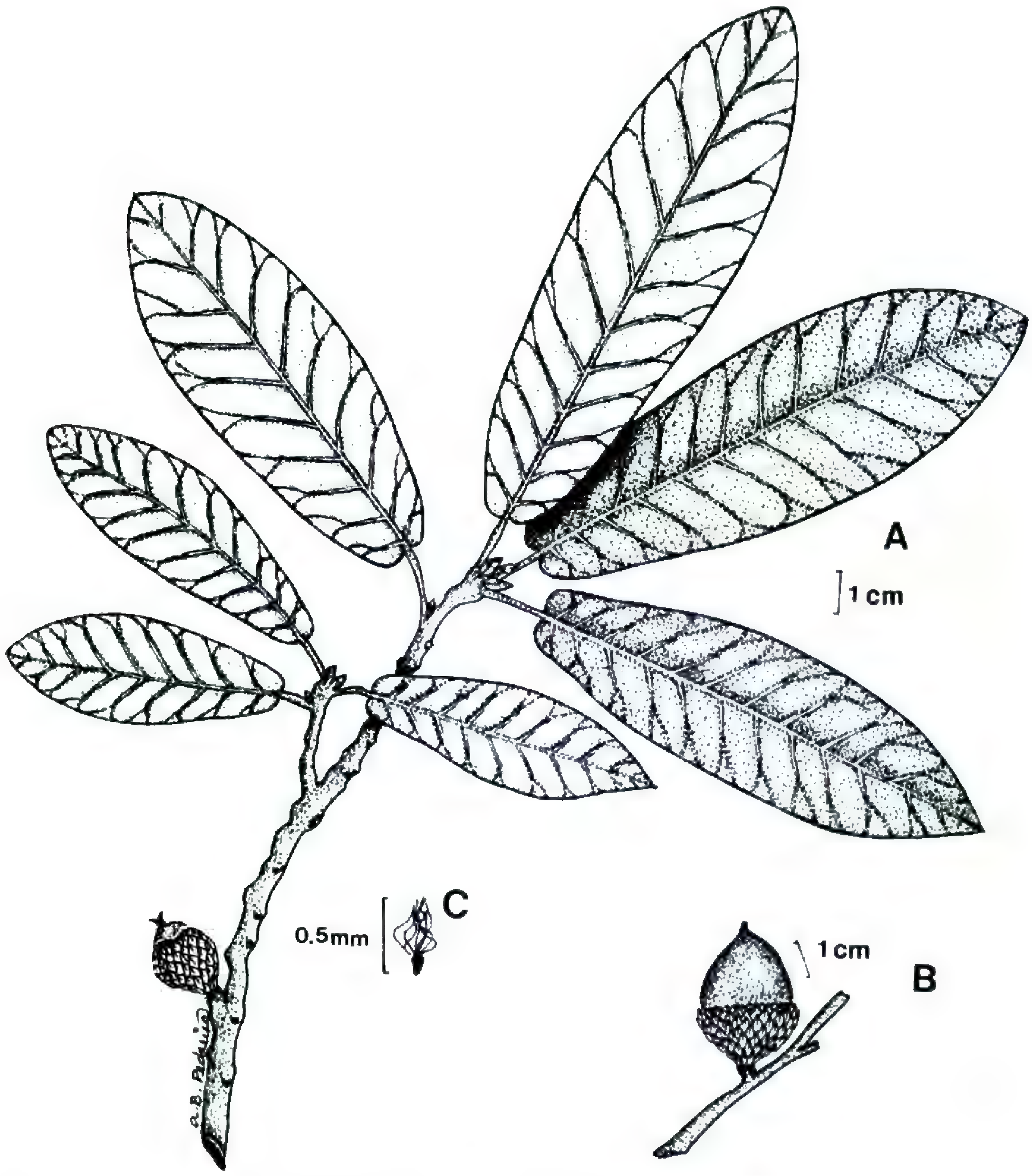

Figura 21. *Quercus mexicana.*—A. Rama. —B. Fruto. —C. Tricoma. (*Quintero 30.*)

nervadura central, ésta impresa o ligeramente elevada, las secundarias impresas; envés ligeramente más pálido, con pubescencia de tricomas estrellados contortos, que se observan como puntuaciones, uniformemente distribuidas, epidermis papilosa; pecíolos pubescentes, de (2–)3–8 mm de largo, de 0.5–1.5 mm diám.; flores desconocidas; fruto anual, solitario o en pares, sésiles o en pedúnculos de 2–9 mm de largo; cúpula hemisférica, de 10–13 mm diám., con las escamas delgadas, no engrosadas en la base, pubescentes, con el ápice subagudo o redondeado, márgenes por lo general glabros; bellota ovoide, pared interna del pericarpo lanosa, de 9–15 mm de largo, de 8–11 mm diám., incluida un tercio o la mitad de su largo en la cúpula. Figura 21.

Discusión. *Quercus mexicana* se reconoce porque sus hojas tienen bordes enteros, ápice aristado y envés con tricomas contortos que se observan como puntuaciones. *Quercus mexicana* muestra similitud con *Q. crassipes,* esta última se distingue por no presentar los tricomas contortos a manera de puntuaciones.

Distribución y hábitat. En México en los estados de Chiapas, Distrito Federal Guanajuato, Hidalgo, Estado de México, Nuevo León, Puebla, Querétaro, San Luis Potosí, Tamaulipas y Veracruz. En bosques de *Quercus* y *Quercus–Pinus,* también en suelos erosionados y a orillas de arroyos, se asocia con *Pinus montezumae, P. leiophylla, P. teocote* y *P. rudis,* en altitudes de 2230–3050 m.

Fenología. Fructifica de julio a enero.

Nombres populares y usos. Encino, encino tezahuatl.

Hasta el momento no se tiene conocimiento sobre sus usos.

Ejemplares examinados. MÉXICO. **Estado de México**: Atizapán, 4 km al N de Atizapán, *Castilla 2723*

(IZTA); Coyotepec, Sierra de Alcaparrosa, *Rojas & Romero 156* (IZTA); Huixquilucan, Fraccionamiento La Herradura, *Domínguez s.n.* (INIF); Jilotepec, Jilotepec, *Matuda 26742* (CODAGEM); Las Peñas, *Rojas & Romero 3076* (IZTA); Ojo de Agua, *Rojas & Romero 3240* (IZTA); Temascalapa, Sierra de Guadalupe P. 3 Padres, *Ortíz s.n.* (IZTA); Cerro Gordo, *Tejero & Castilla 634* (IZTA); Tepotzotlán, Arcos del Sitio, *Ceballos 2* (IZTA); Villa del Carbón, cortina de la presa San Luis Taximay, *Tejero & Abundiz 2766* (IZTA); San Luis Taximay, *Tejero & Castilla 2723* (IZTA); Villa Nicolás Romero, 1 km al E de Lanzarote, *Rzedowski 31877* (INIF); 3 km al NW de Cahuacán, *Rzedowski 32628* (INIF).

22. Quercus scytophylla Liebmann, Overs. Kongel. Danske Vidensk. Selsk. Forh. Medlemmers Arbeider: 180. 1854. TIPO: México. Oaxaca: Yalala a Yagochi, *Liebmann 144–6=3557* (C).

Árbol de 8–20 m de alto, de 30–50 cm diám.; ramillas de 1.5–3 mm diám., grises a castaño rojizo o negras, finamente pubescentes, con tricomas pequeños estrellados; lenticelas pálidas, de 0.5–3 mm de largo; yemas de 1–4 mm de largo, ovoides o elípticas, escamas pubescentes con los márgenes ciliados, engrosadas en la base, de color castaño; estípulas lineares, pubescentes, caedizas, membranosas, de hasta 5 mm de largo; hojas jóvenes pubescentes, haz verde amarillento con tonos cafés, con numerosos tricomas pequeños, estrellados, semejantes a los que se observan en las ramillas, tricomas de mayor tamaño se concentran en la nervadura central; hojas maduras coriáceas, generalmente obovadas, elípticas, oblanceoladas o lanceoladas, lámina (6.2–)8–14.5(–19.5) × (2.3–)4–7(–8.5) cm, ápice con un diente alargado, aristado, base obtusa o cuneada, a veces oblicua, borde engrosado, revoluto, cartilaginoso, con 1 a 7 dientes aristados a cada lado, casi desde la base de la hoja, aristas hasta de 4 mm de largo; nervaduras 5 a 9 primarias en cada lado, rectas o arqueadas, anastomosándose cerca del borde, pasando directamente al diente y luego a la arista, a veces las divisiones de las primeras lo hacen también; haz verde grisáceo, no lustroso, glabro, excepto en la base de la nervadura central, generalmente los tricomas ennegrecidos, nervaduras impresas, el aspecto general es rugoso; envés densamente pubescente, blanquecino, que cambia a amarillento y que se ennegrece con el tiempo, indumento formado por tricomas estrellados con más de 10 rayos, sésiles, epidermis ampulosa y papilosa; nervaduras central y secundarias conspicuamente elevadas, blancas; pecíolos de (0.7–)1–4 cm de largo, de 1–2 mm diám., se engrosan hacia la base, con fina pubescencia gris; amentos masculinos laxos, perianto de 1.5–2 mm diám., glabros, anteras de 1.5 mm de largo, filamentos de 1.5–2 mm de largo; fruto anual, en grupos de dos, sobre pedúnculos de 5–15 mm de largo; cúpula hemisférica, de 10–12 mm diám., escamas delgadas, pubescentes, largamente ciliadas en los bordes, ápices redondeados a agudos, adpresas; bellota ovoide, de 8–10 mm diám., de 10 mm de largo, incluída de un medio a dos tercios de su largo en la cúpula. Figura 22.

Discusión. *Quercus scytophylla* se reconoce por sus hojas dentado-aristadas, haz opaco y envés con pubescencia blanca.

Distribución y hábitat. En México en los estados de Durango, Guerrero, Jalisco, Estado de México, Michoacán, Nayarit, Oaxaca, Puebla, Sinaloa y Sonora. En bosque de *Quercus*, bosque de *Pinus–Quercus* y bosque mesófilo de montaña, se asocia a *Arbutus*, *Pinus oocarpa*, *Pinus teocote*, en altitudes de 900–2500 m.

Fenología. Florece en febrero y fructifica en octubre.

Nombres populares y usos. Encino prieto, encino blanco, encino rosillo.

Su madera se utiliza para la elaboración de trabajos artesanales, así como fuente celulósica de pulpa para papel (González, 1986).

Ejemplares examinados. MÉXICO. **Estado de México**: Amatepec, entre Amatepec y Sultepec, *Matuda & col. 29832* (CODAGEM); Nuevo Santo Tomás de los Plátanos, *Matuda & col. 29387* (ENCB); Sultepec, El Campamento, cerca de Sultepec, *Madrigal 17* (INIF); Las Trojas, *Rodríguez 179* (INIF); Sultepequito, *Rodríguez 181* (ENCB); Tejupilco, Potrero Chico, 15 km al NW de Nanchititla, *González et al. 5436* (ENCB); Peña Bonita, Nanchititla, *Ramos s.n.* (ENCB); 2 km al NW de Nanchititla, *Rzedowski 22177* (ENCB); Temascaltepec de González, km 65 de la carretera Toluca–Temascaltepec, *Casillas 3, 9* (IZTA); Real de Arriba, *Huerta, Ramos & col. RA-6* (ENCB, INIF); presa La Carbonera, *Nah 3652* (ENCB, INIF); km 30 de la carretera federal 130, cercanías de Mesón Viejo, *Orozco 49-B* (IZTA); Real de Arriba, *Ramos & Rocha 96* (INIF); km 51 de la carretera Toluca–San Diego Cuentla, *Rojas & Romero 3212* (INIF); Valle de Bravo, Casas Viejas, *Huerta & col. CV-23* (ENCB, INIF); Valle de Bravo, *Martínez 2604* (ENCB); Zacualpan, km 6 de la carretera Zacualpan–Mamatla, *Fragoso 152* (IZTA); Zacualpan, *Matuda & col. 30298, 30299* (ENCB); km 2–3 de la carretera Campana de Plata–Subestación Coronas, *Tejero & Castilla 1734* (IZTA).

23. Quercus urbanii Trelease, Proc. Amer. Philos. Soc. 60: 32, pl. 2. 1921. TIPO: México. Michoacán a Guerrero, Sierra Madre, 20 June 1899, *E. Langlassé 1066* (B).

Árbol de 4–10 m de alto, tronco de 20–30 cm diám.; ramillas gruesas, con costillas, de 5–11 mm diám., densamente pubescentes, pubescencia amarillenta, gris-amarillenta o negra, formada por

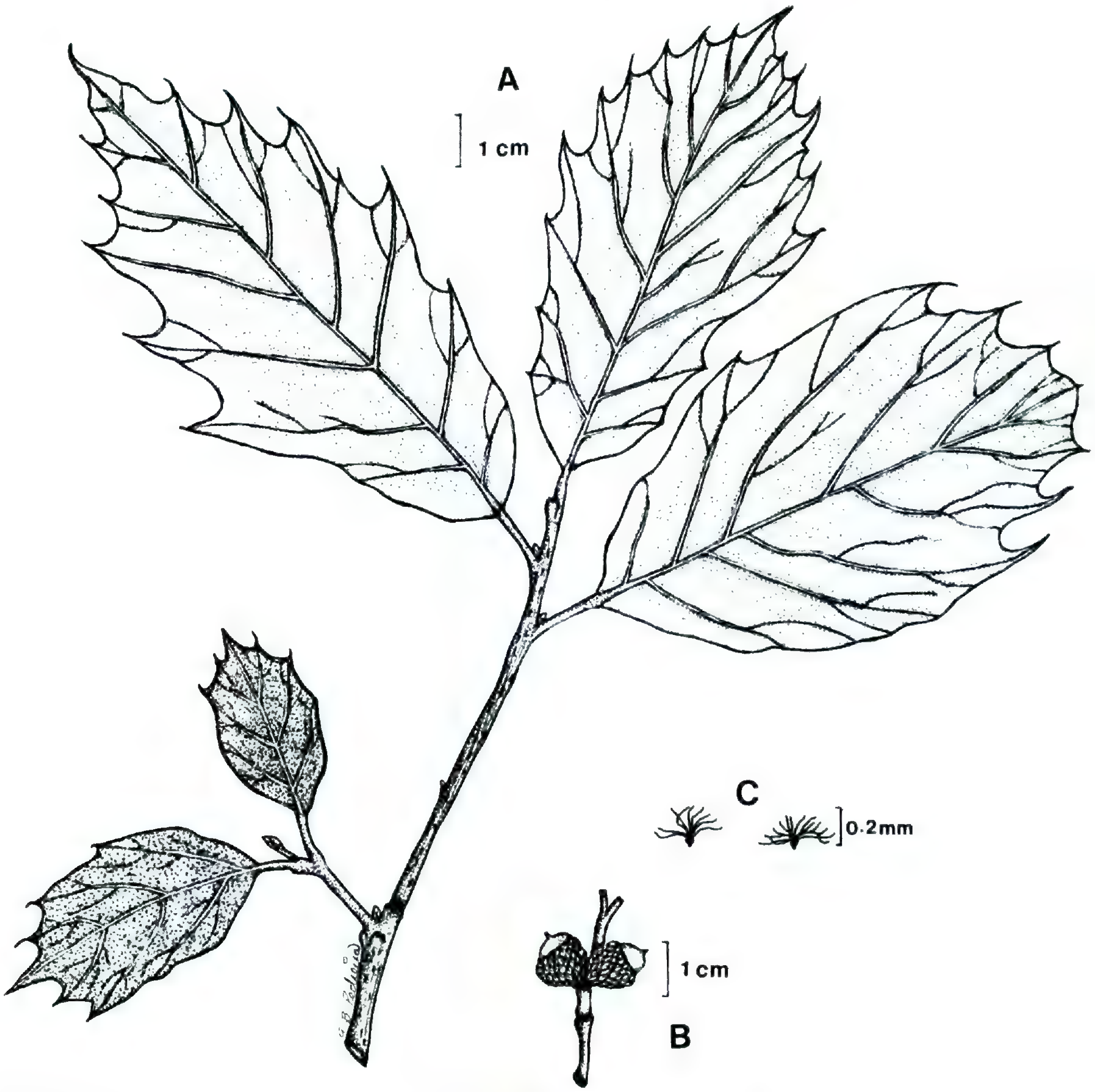

Figura 22. *Quercus scytophylla.*—A. Rama. —B. Fruto. —C. Tricomas. (*Orozco 49b.*)

tricomas estrellados estipitados con las ramas erectas y por abundantes tricomas glandulares sobre la epidermis, corteza castaño-rojiza a negra; lenticelas inconspicuas debido a la pubescencia, en las ramas más gruesas éstas miden hasta 4 mm de largo; yemas de 5–10 mm de largo, ovoides, color castaño, las escamas engrosadas en la base, glabrescentes las exteriores, densamente pubescentes las interiores; estípulas de 7 mm de largo, de 1 mm diám., pubescentes principalmente en la base y bordes, persistentes en las yemas; hojas jóvenes pubescentes, haz cubierto por tricomas glandulares rojizos, tricomas simples dispersos y tricomas estrellados largos, estos últimos principalmente en los bordes, envés con pubescencia blanca formada por tricomas estrellados muy largos; hojas maduras, rígidas, gruesas, panduriformes, obovadas, suborbiculares, orbiculares u ovado-elípticas, lámina (12–)15–30 × (12–)17–34 cm, a veces más larga que ancha, ápice obtuso, a veces algo escotado, base profundamente cordada, borde revoluto, grueso, cartilaginoso, entero, dentado u ondulado, con (5–)10–20 aristas por lado, en las ⅔ partes superiores, a veces desde la base, aristas de hasta 4 mm de largo; nervaduras de 9 a 11 en cada lado, ascendentes, algunas forman directamente las aristas, la mayoría se ramifican cerca del borde; haz verde pálido, algo lustroso, rugoso, glabro, excepto en las nervaduras principales y primarias en donde se encuentran tricomas glandulares simples y estrellados, nervaduras impresas a ligeramente elevadas; envés con tomento de aspecto lanoso, amarillento, formado por tricomas estrellados, estipitados con rayos de hasta 3 mm de largo, enredados, cubriendo uniformemente la epidermis papilosa y glandulosa, nerva-

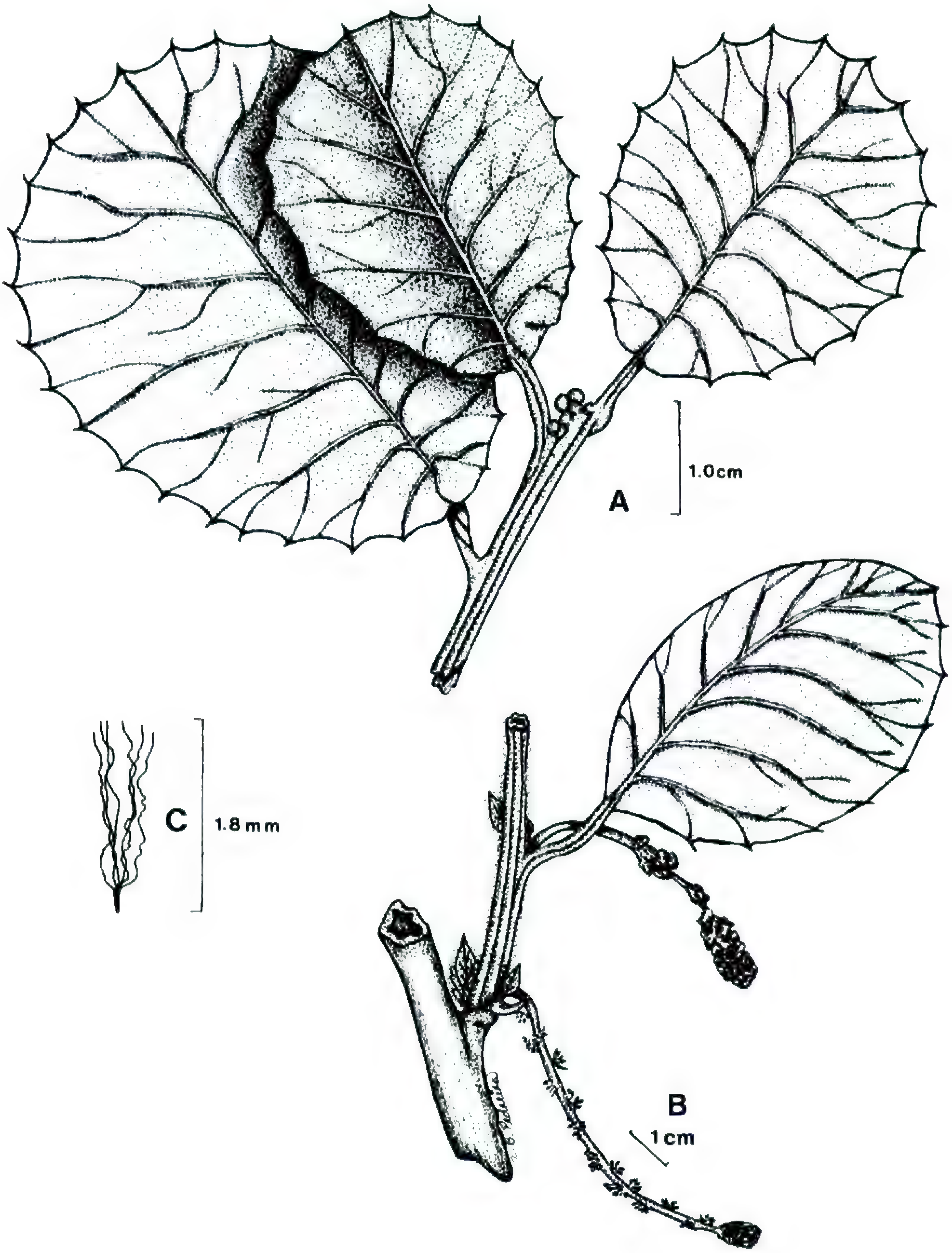

Figura 23. *Quercus urbanii.*—A. Rama. —B. Inflorescencias masculinas. —C. Tricoma. (*Torres 197*; *González 5017*.)

duras elevadas; pecíolos de 3–4 cm de largo, de 2–4(–6) mm diám., tomentosos, se ennegrecen con la edad; amentos masculinos de 13–23 cm de largo, raquis densamente tomentoso, perianto de 6 mm diám., glabro, excepto los bordes de los lóbulos que son ciliados, anteras apendiculares, de 2–2.5 mm de largo, filamentos de 2 mm de largo; amentos femeninos de 10 a 20 flores en pedúnculos gruesos, con tomento abundante de color amarillo; frutos en grupos de 5 a 10 o más, en pedúnculos de 7.5–9 cm de largo, de 4–5 mm diám., con denso tomento amarillento que se obscurece y cae con el tiempo; cúpula de 8–12 mm diám., escamas pubescentes con los ápices redondeados a truncados; bellota ovoide, pared interna del pericarpo lanosa, de 10 mm de largo, de 8–10 mm diám., incluída de un tercio a un medio de su largo en la cúpula. Figura 23.

Discusión. Se reconoce por sus hojas grandes,

acucharadas, el tomento del envés amarillo y sus ramillas gruesas.

Distribución y hábitat. En México en los estados de Durango, Guerrero, Jalisco, Estado de México, Nayarit, Sonora y Zacatecas. En bosques de *Pinus–Quercus* y bosque mesófilo de montaña, asociado con *Quercus scytophylla, Q. crassifolia, Q. obtusata, Q. laurina, Pinus montezumae, P. pseudostrobus, P. oocarpa* y *Alnus,* en altitudes de 1400–2500 m.

Fenología. Florece en diciembre y fructifica en octubre.

Nombres populares y usos. Encino.

Su madera se usa como leña (González, 1986); se sabe que también es utilizada para la elaboración de arados y los frutos sirven para alimentar ganado porcino (Vázquez, 1992).

Ejemplares examinados. MÉXICO. **Estado de México**: Sultepec, entre Sultepec y el paraje El Campamento, *Madrigal 25* (ENCB, INIF); La Cieneguilla, *Rodríguez 161* (INIF); km 12 carretera Sultepec–San Miguel Totolmoloya, *Torres 197* (IZTA); km 18 carretera Sultepec–San Miguel Totolmoloya, *Torres 428* (IZTA); Tejupilco, 5 km al SW de Nanchititla, *González 5017* (ENCB); Los hormigueros, Nanchititla, *Hernández 1747* (INIF); 12 km de El Corupo a Nanchititla, *Rojas & Romero 3955* (IZTA); Puerto del Embocadero, 7 km al W de Luvianos, *Rzedowski 22126* (ENCB, INIF); Nanchititla, alrededores de la Población, *Rzedowski 30307* (ENCB); Zacualpan, Zacualpan, *Matuda 30314* (CODAGEM).

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